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New Zealand Recent Densiporidae and Lichenoporidae (Bryozoa: Cyclostomata)

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This paper describes Recent cyclostome bryozoans of the families Densiporidae and Lichenoporidae in the New Zealand region. The Densiporidae are recognised as a family with interior-walled autozooids, exterior-walled brood-chambers, and kenozooids lacking diaphragms. In New Zealand, the family comprises five species of *Favosipora*, of which four are new (*F. candida*, *F. marmorosa*, *F. rosea*, *F. tincta*). The generic status of *Favosipora* is clarified, and its scope expanded to include nine species, of which only one extends into the Northern Hemisphere. Four new combinations are introduced: *Favosipora holdsworthii* (Busk, 1875), *F. nanzoifera* (Moyano, 1982), *F. otagoensis* (Taylor, Schembri and Cook, 1989), and *F. watersi* (Borg, 1944). New Zealand Lichenoporidae presently comprise five species of *Disporella*—two new (*D. humilis*, *D. sacculus*), and one new species of *Doliocoitis* (*D. cyanea*). *Disporella buski* Harmer, 1915 and *D. gordonii* Taylor, Schembri and Cook, 1989 are synonymised with *D. pristis* (MacGillivray, 1884). Sabri's (1988) synonymising of *Disporella novaezelandiae* (Busk, 1875) with *D. novae-hollandiae* (d'Orbigny, 1853) is accepted.

Key Words: New Zealand, Bryozoa, Cyclostomata, Densiporidae, *Favosipora*, Lichenoporidae, *Disporella*, *Doliocoitis*, new species, new combinations.

Introduction

The Recent cyclostome bryozoan fauna of the New Zealand region is very little known. The earliest record was that of John Edward Gray (1843), Director of the British Museum (Natural History) and Keeper of the Zoological Collections, who reported on a collection of bryozoans made in New Zealand in 1841 by medical doctor Andrew Sinclair—“*Tubulipora patellata*. Lamx. Inhabits New Zealand.” The identity of this species is not known with certainty [*T. patellata* Lamarck, 1816, *non* Lamouroux, was apparently based on a fish scale—see Edwards (1838: 332)], but Frederick Wollaston Hutton, who made the next listing of New Zealand bryozoans (Hutton 1873), cited Gray's record as *Patinella verrucaria* (Fabricius, 1780), a northeastern Atlantic lichenopoid. This suggests that it may have been *Dis-*

porella novaehollandiae (d'Orbigny, 1853), one of the commonest New Zealand cyclostomes, often found on beach-cast *Sargassum*, except that Hutton (1891, 1904) subsequently referred to this record as *Diastopora patina* (Lamarck, 1816) (i.e., *Plagioecia*), evidently following Busk's (1875: 29) synonymy. (*Plagioecia patina* is not known in New Zealand.) It is not clear, therefore, which species Gray had before him. Hutton (1873) listed 17 nominal cyclostome species (Tubuliporina 10, Rectangulata 2, Cancellata 3, Articulata 2), using European names for many. Of his six new species, none illustrated, two are not currently recognisable (*Tubulipora glomerata*, *A. disposita*), one is a junior synonym (*Hornera squamosa* = *H. foliacea* MacGillivray, 1869), and one is a cheilostome (*Pustulipora porcellanica* = *Galeopsis porcellanicus*). Hutton (1880) corrected some of the names and added another new tubuliporine species to the list—*Defranceia dentata*—to replace *Tennysonia stellata* Busk, 1867 included in error by Hutton (1873). New Zealand cyclostomes were listed in subsequent works by Hutton (1877, 1880, 1891, 1904) and Hamilton (1898), but it is not easy to harmonise the various names used in these checklists. Suffice it to say that, by 1904, Hutton listed 29 Recent New Zealand cyclostomes [cf. 32 species in Hamilton's (1898) list]. These included four nominal lichenopodid species.

Very little taxonomic work was carried out on New Zealand Recent cyclostomes during the rest of the twentieth century, although they were mentioned in some ecological studies and faunal reviews (e.g., Morton and Miller 1968; Ryland 1975; Gordon and Ballantine 1977; Taylor 1991, 1994; Gordon and Mawatari 1992). Taxonomic papers describing or redescribing New Zealand Recent cyclostomes were those of Taylor *et al.* (1989) (hermit-crab associates), Boardman *et al.* (1992) (Cinctiporidae), Taylor and Gordon (1997) (a new tubuliporine genus), and Taylor and Gordon (2001) (*Liripora* and *Mesenteripora*). We have compiled an interim species checklist based on personal collections and those housed in the National Institute of Water & Atmospheric Research (Wellington), the Museum of New Zealand (Wellington), the Otago Museum (Dunedin), and The Natural History Museum (London). We estimate 100 living species in the New Zealand 200 nautical mile Exclusive Economic Zone (EEZ)—Tubuliporina 64, Cerioporina 12, Rectangulata 13, Cancellata 5, Articulata 6.

This paper deals with two families (Densiporidae and Lichenoporidae) of taxonomically difficult species that, although conventionally placed in different suborders (Cerioporina and Rectangulata, respectively), have a number of morphological features in common. The form of the colony in some densiporids is so similar to that of some lichenoporids that it is sensible to treat the species together and formulate a common key. Not all lichenoporids are dealt with here, however. Some likely new species in the above-mentioned collections are represented by infertile and/or small colonies or very few specimens. These are mostly from the continental shelf and deep sea and are rarely encountered. They will be described at a later date when additional material comes to hand.

Materials and Methods

The species described were studied by scanning electron microscopy (SEM), using type and other specimens. Sorted material was soaked in sodium hypochlo-

rite solution overnight, then washed in water. Specimens photographed in New Zealand were gold-coated and imaged using secondary electrons in a Philips SEM at the Institute of Geological & Nuclear Sciences, Lower Hutt. Specimens photographed in London were left uncoated and examined in an environmental chamber with a back-scattered electron detector attached to an ISI ABT-55 SEM at The Natural History Museum. Morphometric determinations were made through the use of eyepiece micrometers or from micrographs.

Specimen repositories and abbreviations: NIWA, National Institute of Water & Atmospheric Research, Wellington; NHM, The Natural History Museum, London.

Systematics and Distribution

Family Densiporidae Borg, 1944

Densiporidae Borg, 1944: 209.

Revised diagnosis. Colony encrusting, sometimes thickly, or small and pedunculate; radially symmetrical or, if extensive, with macular centres. Autozooids and kenozooids free-walled (lacking calcified exterior frontal walls), although some autozooidal peristomes fixed-walled. Autozooids arranged radially or quincuncially, flanked or surrounded by kenozooids lacking diaphragms. Brood-chamber roof exterior-walled, entire or pierced by autozooidal peristomes, densely pseudoporous, and typically bordered by raised rim; oeciostome relatively simple tube, oeciopore generally simple, sometimes slightly flared.

Remarks. In a discussion of the cyclostome suborder Heteroporina (=Cerioporina), Borg (1944) proposed the family Densiporidae, based on the relatively little-known Australian type genus, *Densipora* MacGillivray, 1881. MacGillivray (1881: 17) assigned monotypic *Densipora* to the Diastoporidae, then somewhat heterogeneous in composition, remarking: "The examination of full-grown individuals would leave the exact position of this species doubtful, but an inspection of young specimens shows its Diastoporidan characters. The smallest specimen I have is about one-twentieth of an inch [1.27 mm] in diameter, is discoid, of considerable thickness in the centre, with the cells closely connate, vertical in the middle, and oblique toward the circumference." In a checklist of Victorian Bryozoa published six years later, MacGillivray (1887) transferred *Densipora* to the Discoporellidae (=Lichenoporidae), but twentieth-century authors have included it among the genera of Heteroporidae (=Cerioporidae) (e.g., Borg 1933; Bassler 1934, 1953). The family name Densiporidae, scarcely used since Borg (1944), was provisionally reincluded in the Cerioporidae by Taylor (1993), and fully reinstated by Taylor and Weedon (2000).

MacGillivray (1885, 1887) introduced two other novel Victorian genera of Cyclostomata—*Favosipora* and *Flosculipora*, both of which he included in the Discoporellidae/Lichenoporidae, as did Bassler (1934, 1953). These two genera, also poorly known, are represented in the collection of The Natural History Museum, London, and we have been able to examine them. All three genera (*Densipora*, *Favosipora*, *Flosculipora*) have an exterior-walled brood-chamber and kenozooids that lack terminal diaphragms. Their morphological characters and geographic distribution are such that we here regard them as being confamilial, i.e., densi-

porids. *Densipora* and *Flosculipora* have not been discovered in the New Zealand region, but there are several hitherto undescribed species of *Favosipora*, which vary from small, discoidal, and more or less radially symmetrical to large crusts with numerous maculae.

The skeletal morphology of densiporids is in some ways intermediate between that of cerioporids and lichenoporids. The exterior-walled brood-chamber is typical of cerioporids. On the other hand, the radial arrangement of autozooids, with interspersed kenozooids, in some species of *Favosipora* is very like that of many lichenoporids. Weedon and Taylor (1996) studied skeletal ultrastructure in a range of cerioporine taxa, including *Favosipora*, which resembles rectangulates in having interior walls of a foliated fabric. The occurrence of secondary nanozooids in two species of *Favosipora* is, on the other hand, a character more usually associated with tubuliporines.

Genus *Favosipora* MacGillivray, 1885

Favosipora MacGillivray, 1885: 98.

Type species. *Favosipora rugosa* MacGillivray, 1885: 98, by monotypy.

Revised diagnosis. Colony adnate, simple, and radial, or large and irregular. Autozooids interior-walled, arranged quincuncially or radially, separated by kenozooids. Autozooidal peristomes simple, cusped, or nodular, sealed in some species by perforated or imperforate closure plates and occasionally becoming transformed into secondary nanozooids. Kenozooids not closed by terminal diaphragms. Brood-chamber expanded gonozooid with granulated floor; roof exterior-walled and densely pseudoporous, oeciostome short, relatively simple. Ancestrula and early generations of daughter zooids soon concealed by reflexed marginal lamina.

Remarks. Though distinctive, *Favosipora* is a poorly known genus, mainly found in the Southern Hemisphere. Most species resemble lichenoporids but are readily distinguished from them by the exterior-walled brood-chamber. A notable example is *Favosipora holdsworthii* (Busk, 1875), **comb. nov.**, originally classified in *Discoporella* (i.e., *Disporella*) (Busk 1875; Alvarez 1992), and often in *Lichenopora* (e.g., Waters 1889; Borg 1944). Alvarez (1992, fig. 16C) illustrated by SEM a fertile specimen from the type series, demonstrating clearly the exterior-walled nature of the brood-chamber roof. *Favosipora holdsworthii* appears to be the only Northern Hemisphere species (type locality: Sri Lanka). MacGillivray (1885: 98) included *Favosipora* in the Discoporellidae (i.e., Lichenoporidae) but remarked: "This genus is evidently allied to *Densipora corrugata*." We agree. Other species that may be re-assigned to *Favosipora* include *Lichenopora watersi* Borg, 1944 and *Disporella nanaoifera* Moyano, 1982. The brood-chamber of southern Australian (Western Australia to Victoria) *Favosipora watersi*, **comb. nov.** was described and illustrated by Waters (1889) [in error as *Lichenopora californica* (d'Orbigny, 1853)] as a "finely perforated plate". Silén (1954) also described and illustrated this species, showing the brood-chamber and mentioning the pale pink colour of the colony. Chilean *Favosipora nanaoifera*, **comb. nov.**, with "whitish" colonies, was perceptively compared with *Favosipora* by Moyano (1982), who discussed the significance of the nanozooids in this putative lichenopodid.

MacGillivray's (1885) illustrations of the type species, *F. rugosa*, leave much to be desired. Fertile colonies in the collection of the NHM are reddish in colour and somewhat robust, exceeding one centimetre in diameter. Autozooids are mostly connate in rows or fascicles and surrounded by moderately thick-walled kenozooids. These do not develop terminal diaphragms but some autozooids associated with brood-chambers have perforated closure plates. Brood-chambers are exterior-walled and densely pseudoporous, with a distinct, somewhat expanded, margin. The oeciostome is simple and circular.

***Favosipora candida* sp. nov.**
(Figs 1–8)

Disporella sp. 1: Gordon and Ballantine 1977: 124.

Material examined. NIWA holotype H-739, from Stn Z9684; NIWA paratype from Mission Bay, Auckland; also colonies in D. P. Gordon collection from Auckland, Goat Island Bay (Leigh), and NIWA Stns D269, D270, D273, Z8468, Z8645, Z9673. Also NHM 1944.11.10.1 from ?Auckland.

Etymology. From the Latin, *candidus*, white, bright.

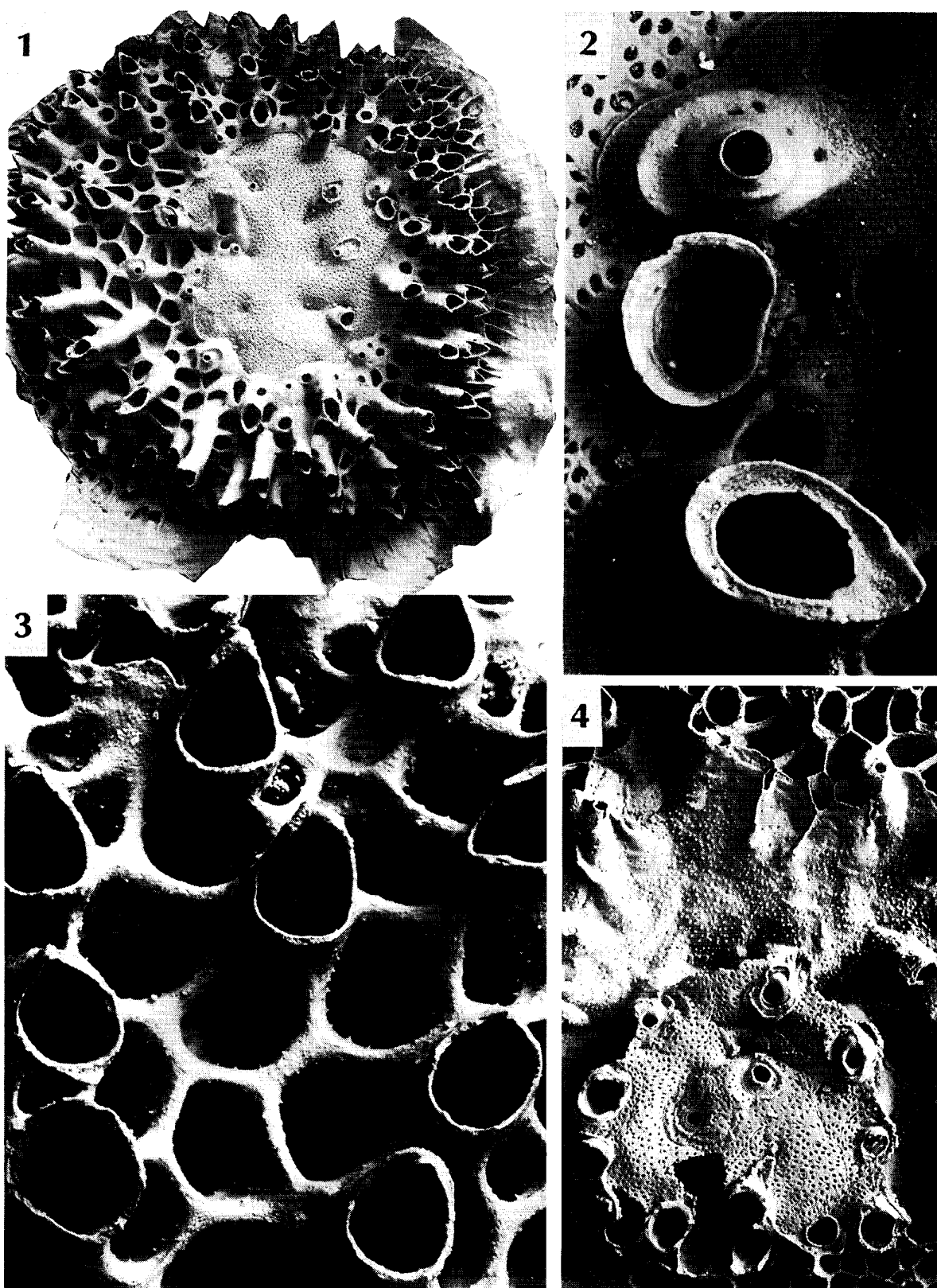
Description. Colony adnate, with marginal lamina; white, simple, circular, and more or less radially symmetrical with single macular centre, to large with up to ~30 monticular maculae. Maculae variable in size and spacing. In small, infertile colonies of <1.70 mm diameter, colony centre occupied mostly by kenozooids with polygonal outlines, but this arrangement disturbed by early development of 1–2 gonozooids in central area of colony, resulting in macular centre surrounded by autozooidal peristomes. Large colonies with low-mounded maculae ~1.32–1.89 mm in diameter with centre-to-centre spacing of ~1.45–1.60 mm; some monticules so close as to form short ridges. Smallest brooding colonies ~1.80 mm in diameter; largest colony seen, 15.2 mm in maximum diameter including narrow lamina. Colonies usually developing more or less evenly outwards; one large colony from NIWA Stn Z8645 evidently interrupted in development so as to become more lobate than radial, boundaries between contiguous adjacent lobes evident as narrow vertical rim (Figs 5, 7).

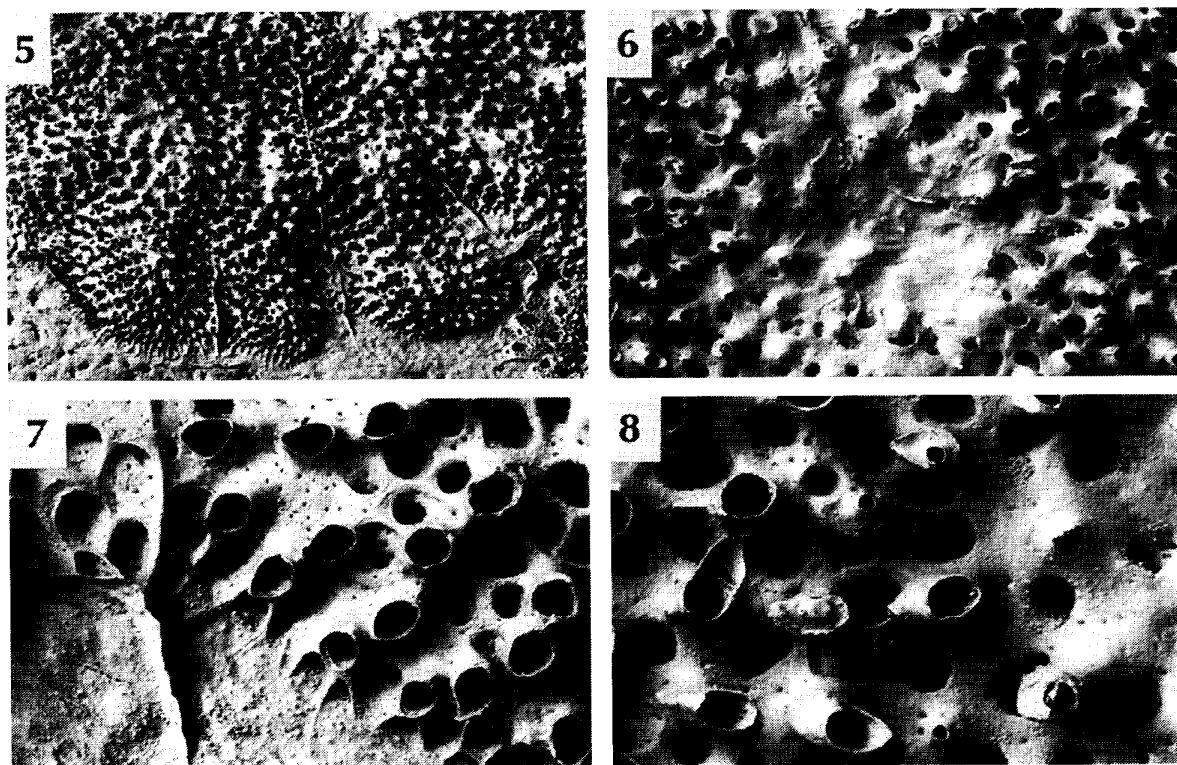
Macular kenozooids in small colonies with relatively large internal diameter (up to 0.15 mm) before their walls thicken, but kenozooids in general of variable diameter (0.035–0.068 mm) and smaller than autozooidal apertures in large, brooding colonies. In parts of colonies with kenozooidal openings reduced by calcification filling in spaces between autozooidal peristomes, pores evident in calcification.

Autozooids arranged quincuncially. Peristomes 0.090–0.094 mm in diameter, bicuspid, rim produced upward on admacular and abmacular sides in small colonies, peristomes and cusps generally shorter or even absent in large colonies.

Nanozooids secondarily developed from autozooids (rarely from kenozooids?) by formation of perforated terminal diaphragm and small, projecting tube with opening 0.020 mm in diameter. These sporadically distributed, often around or within gonozooids, less common elsewhere.

Marginal lamina and zooidal interiors granular to minutely pustulose. Skeletal ultrastructure of imbricating platey crystallites. Septa marking boundaries of





Figs 5–8. *Favosipora candida* sp. nov., NIWA Stn Z8645, Spirits Bay: 5, margin of large, lobate colony, $\times 6$; 6, macula centre with apertures closed by lamina of interior-wall calcification, $\times 26$; 7, growing edge showing development of low, vertical wall at boundary between lobes, $\times 61$; 8, autozooids, some with peristomes, and secondary nanozooids, $\times 64$.

future vertical walls variably developed on marginal lamina.

Brood-chambers with roof densely perforated by tiny pseudopores, these with 8–11 radial spokes. Contiguous brood-chambers separated by double wall and perforated by numerous pores. Both small and large colonies with up to three brood-chambers, these subcircular to somewhat irregular in shape, with maximum diameter 1.73 mm and minimum diameter 0.94 mm. Oeciostome oval, slightly elevated and occasionally a little flared, smaller than an autozooidal peristome, 0.067–0.077 mm in diameter.

Ancestrular protoecium 0.17 mm wide. Ancestrular peristomes and those of first group of zooids inclined more horizontally than vertically and soon concealed by backwardly (proximally) growing marginal lamina of later zooids.

Brood-chamber formation. Brood-chambers are gonozooids. They become

Figs 1–4. *Favosipora candida* sp. nov. 1–2, NHM 1944.11.10.1 from ?Auckland: 1, whole small colony with brood-chamber, oeciostome at right, $\times 36$; 2, close-up of edge of brood-chamber showing, from top, nanozooid, oeciostome, and autozooidal aperture with incipient calcification around rim, $\times 300$. 3, D. P. Gordon collection, unregistered, from lower intertidal, Goat Island Bay, Leigh, showing free-walled autozooidal peristomes and kenozooids, $\times 180$. 4, D. P. Gordon collection, unregistered, from drift *Sargassum sinclairii* laminae, Mission Bay, Auckland, showing granular floor of brood-chamber and part of roof, $\times 66$.

apparent when there are at least 25–35 autozooids; therefore, they are initiated even earlier in astogeny. Developing brood-chambers, often one but more usually two, are recognisable as calyciform depressions at or near the centre in small colonies, at the bottom of which the opening of the female zooid is overhung by a cusped projection of the lateral wall. The granulated floor of the developing brood-chamber spreads outwards across surrounding kenozooids, either spreading around tall autozooidal peristomes or, as the floor thickens in the vicinity of short autozooidal peristomes, inducing the development of terminal closure plates with short tubes so as to form nanozooids. Before the brood-chamber floor is complete, the roof starts to form on one side; the oeciostome may be initiated here or develop later in the centre.

Remarks. *Favosipora candida* is known from Spirits Bay in the far north of North Island, Auckland Harbour, and Cook Strait, from depths of 0 to 85 m. It is found on shell and rock gravel and occurs commonly on *Sargassum sinclairii* Hook. f. and Harv. in Auckland Harbour. Whitten (1979) additionally reported colonies (as *Disporella* sp. nov.) on holdfasts of the laminarian *Ecklonia radiata* (C. Agardh) J. Agardh, red algae, gastropods, brachiopods, glass, and the erect cheilostome *Steginoporella neozelanica* Harmer, 1900.

The formation of the brood-chamber has not been described before in *Favosipora*. Floor development is similar to that in the cerioporine *Heteropora parapelliculata* (Taylor *et al.* 1989, fig. 4D) and in the rectangulate *Disporella hispida* (Schäfer 1991, pl. 40, fig. 4). The exterior-walled brood-chamber roof through which autozooidal peristomes pass is typical of cerioporines.

The occurrence of secondary nanozooids is noteworthy. These are found also in *F. nanozoifera* (Moyano, 1982) but primary and secondary nanozooids are best known in the tubuliporine genera *Diplosolen* and *Plagioecia*, respectively. In *Diplosolen* the primary nanozooids contain a dwarf polypide with a single sweeper tentacle that appears to perform a cleaning function. The single tentacle in the secondary nanozooids of *Plagioecia* is too short to sweep and its function is unknown (Silén and Harmelin 1974).

***Favosipora marmorosa* sp. nov.**

(Figs 9–15)

Material examined. NIWA holotype H-740 and paratypes P-1207, P-1208 from NIWA Stn Z9684; also colonies from NIWA Stns Z8468, Z8664, Z9667, Z9701, Z9705, Z9707.

Etymology. From the Latin, *marmorosus*, marbled or marble-like, alluding to the marbled coloration of the colony.

Description. Colony adnate, simple, circular, and more or less radially symmetrical, comprising single maculum, to large and mounded, up to 16 mm in longest dimension with up to ~37 maculae. In small infertile colonies of ~3.0 mm diameter, colony centre mounded and occupied by kenozooids with polygonal outlines and autozooids with rounded outlines, and bordered by steeply sloping zone of quincuncially arranged, emergent autozooidal peristomes surrounded by kenozooids. Large colonies comprising white maculae formed of kenozooids flanked by purplish-brown troughs of autozooids. Maculae varying in size from somewhat cir-

cular and ~ 0.75 mm in diameter to large and elongate, ca. $3.0\text{ mm} \times 2.0\text{ mm}$, with centre-to-centre spacing of $\sim 1.60\text{--}2.00$ mm. Marginal lamina well developed.

Kenozooids relatively small, of variable apertural diameter ($0.037\text{--}0.091$ mm).

Autozooids arranged quincuncially, apertures circular, $\sim 0.068\text{--}0.091$ mm in diameter, or oval, $\sim 0.083 \times 0.11$ mm in diameter; smallest autozooidal diameters in centre of very small colonies. Peristomes bicuspid or unicuspid, rim produced further on abmacular side.

Nanozooids absent.

Marginal lamina and zooidal interiors very sparsely granular to minutely pustulose. Skeletal ultrastructure of imbricating platey crystallites.

Brood-chambers with very irregular outlines and penetrated by numerous autozooidal peristomes, often connate. Roof densely perforated by tiny pseudopores lacking spokes. Large colonies with up to five brood-chambers externally visible, these minimally ~ 1.23 mm in diameter, or larger and longer than wide, from $\sim 2.07\text{--}2.66 \times 0.94\text{--}1.89$ mm. Oeciostome smaller than adjacent autozooidal apertures, simple, oval, 0.064 mm in widest dimension. The older the brood-chamber, the more sunken in the colony, until concealed by overgrowth of adjacent autozooids and kenozooids or by self-overgrowth of another part of same colony. Cross sections of colonies clearly revealing concealed zooidal layers.

Ancestrula not seen.

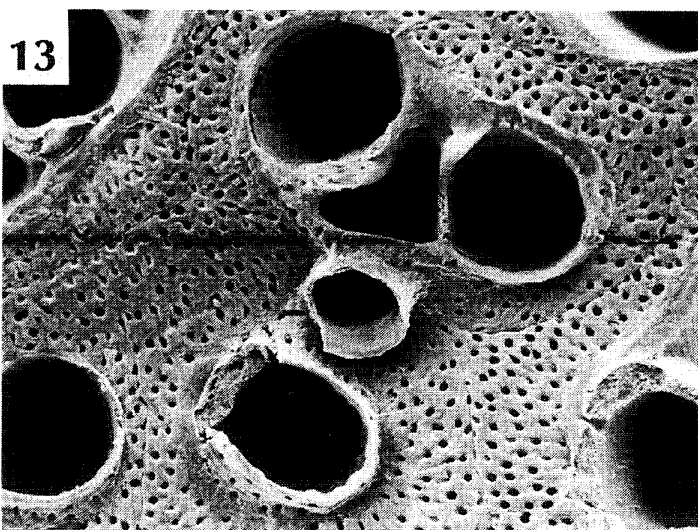
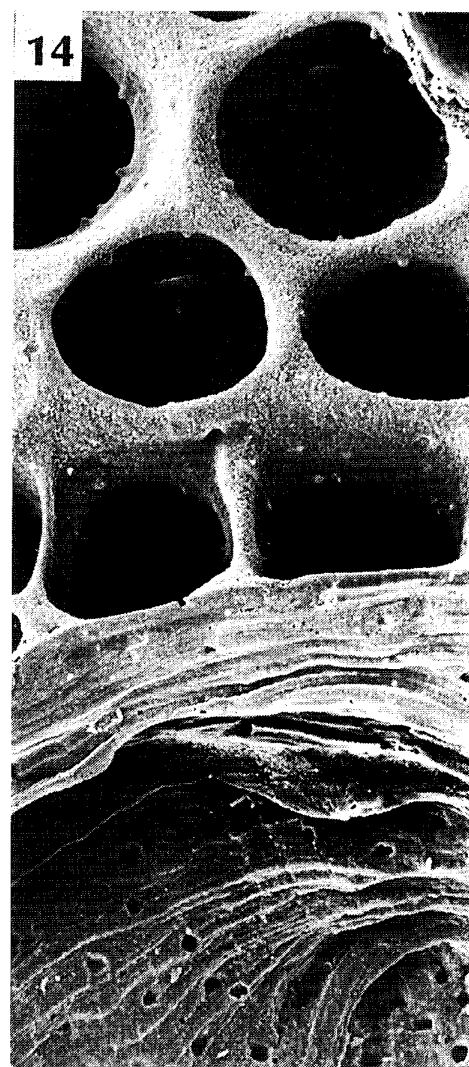
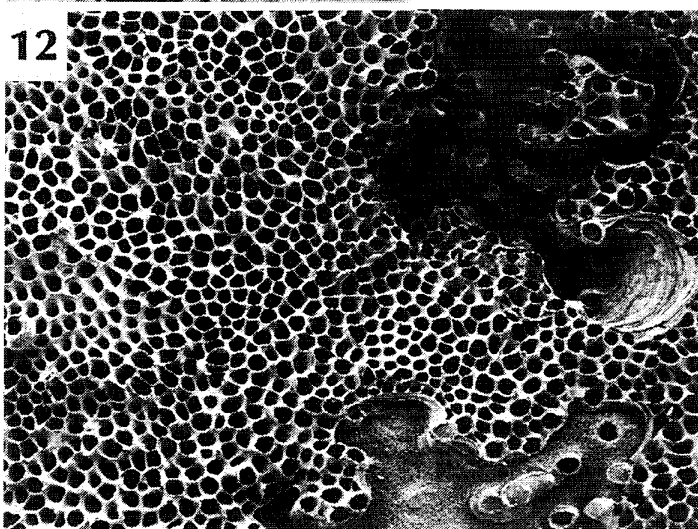
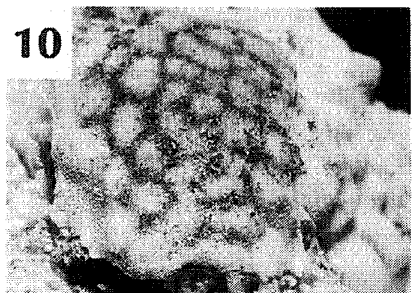
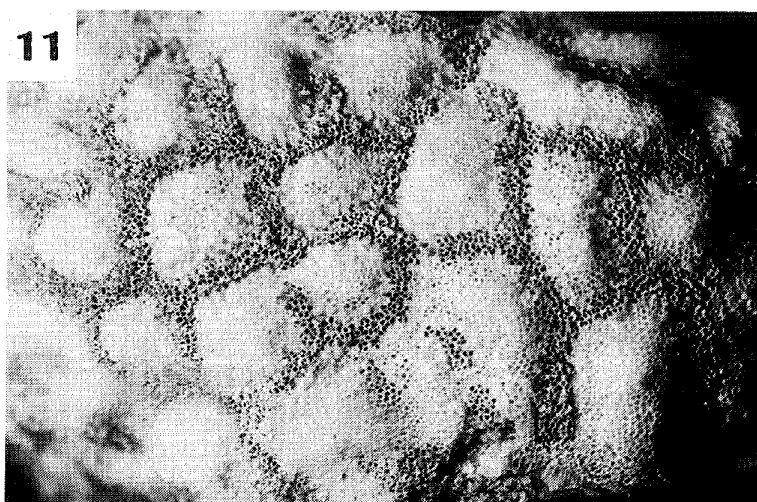
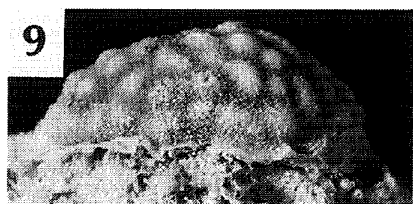
Remarks. *Favosipora marmorosa* is known only from Spirits Bay in the far north of North Island, where it encrusts dead glycymerid mollusc shells from depths of between 29 and 83 m. The bryozoan is striking in the pattern of its pigmentation and the degree of self-overgrowth, resulting in mounded colonies of several layers. Overgrowth can begin in colonies as small as 3–4 mm diameter. Also striking is the ability of autozooids and kenozooids to elongate frontally so as to overtop, and then overgrow, adjacent brood-chambers, which become increasingly sunken in the colony surface.

Favosipora otagoensis (Taylor, Schembri and Cook, 1989), comb. nov.

Borgiola otagoensis Taylor, Schembri and Cook, 1989: 1070, figs 3E, 5C–F.

Material examined. Holotype, NHM 1988.3.1.540; paratypes NHM 1988.3.1.1, 372, 376, 381, 515, Otago Shelf; NIWA Stn B221.

Remarks. *Favosipora otagoensis* is known only from gastropod shells tenanted by hermit crabs [*Lophopagurus foresti* McLaughlin and Gunn, 1992, *L. laurentae* McLaughlin and Gunn, 1992, and *L. stewarti* (Filhol, 1883)] (Forest *et al.* 2000), and may be an obligate symbiont. It was first assigned to *Borgiola* Strand, 1933, a replacement for the preoccupied name *Canuella* Borg, 1933, a monotypical genus proposed for *C. rugosa* Borg, 1933, an erect, branching species from Japan. The chief characters of the genus and type species by which Borg (1933) distinguished it from other cerioporines were the rugose colony surface with monticules, oblique autozooidal apertures, and a (putative) concealed, interior-walled brood-chamber. The Otago species, in contrast, is wholly encrusting, its autozooidal apertures have no processes, and the brood-chamber is exterior-walled. *Borgiola glabra* Androsova, 1965, from the northern Sea of Japan, has an erect



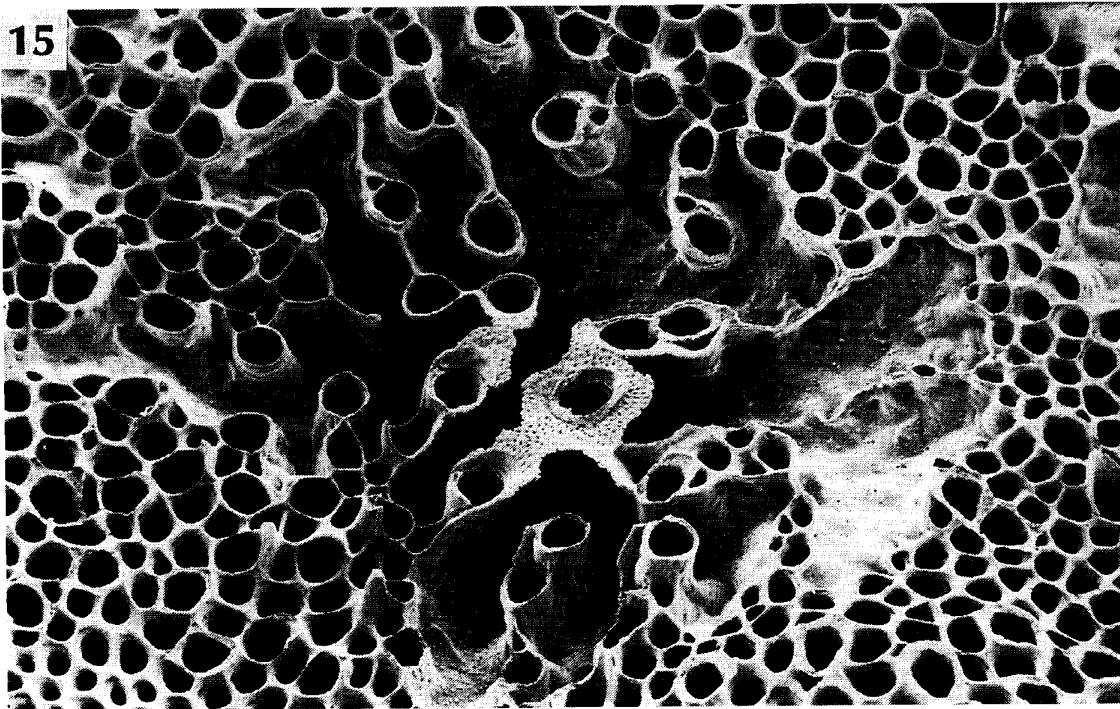
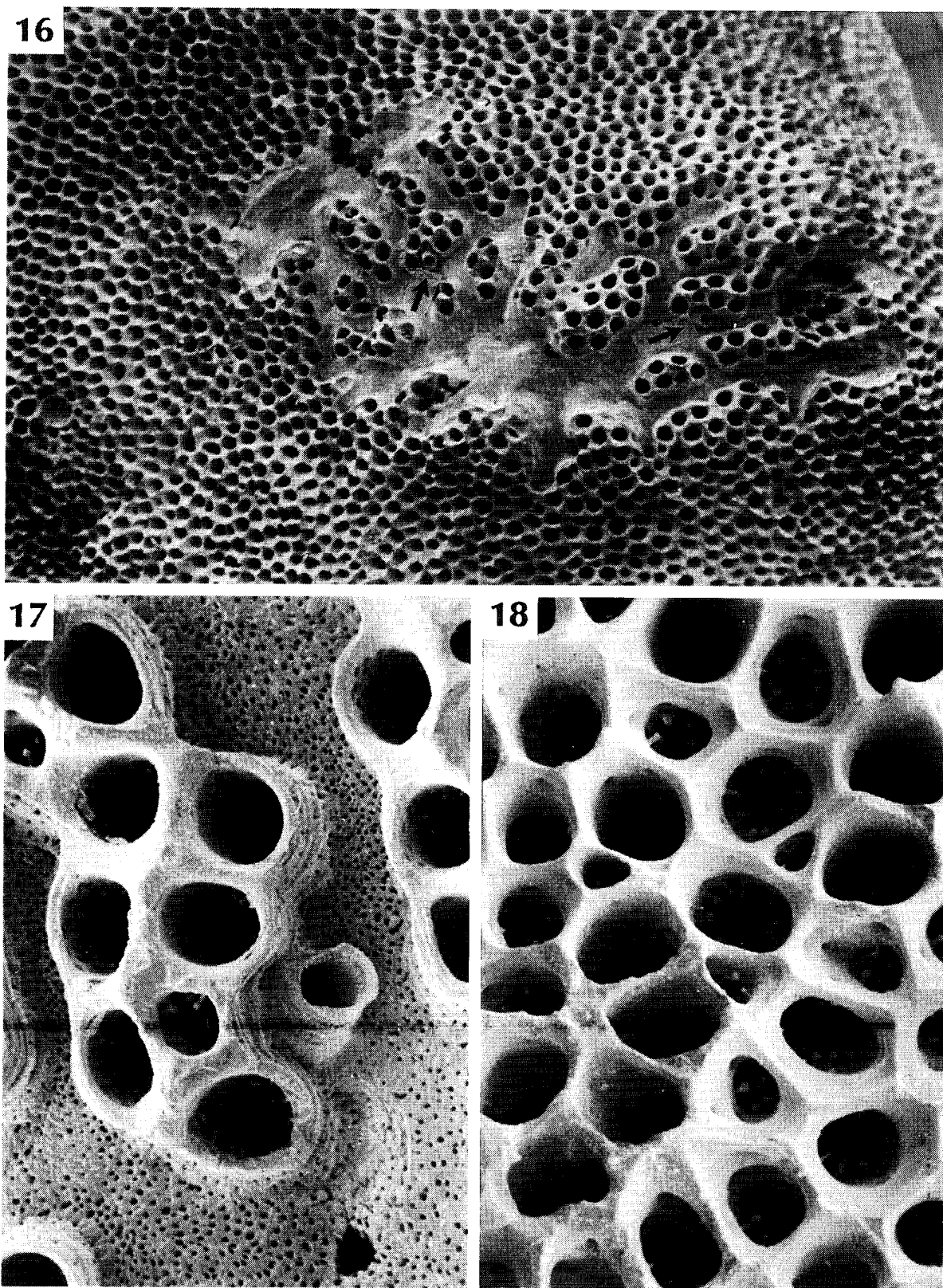


Fig. 15. *Favosipora marmorosa* sp. nov., NIWA Stn Z8664, off Whangaroa Harbour, a developing brood-chamber, its overall calyciform shape typical of early stages of brood-chamber formation, $\times 58$.

colony form and rugose colony surface, thereby resembling the type species, *B. rugosa*, but it has an exterior-walled brood-chamber pierced by autozooidal peristomes (Androsova 1965, fig. 30). There is some doubt about the nature of the brood-chamber in *B. rugosa*—Borg's (1933, pl. 12, fig. 2) illustration of this putative character is not convincing and Borg himself was not sure if the indicated cavity really was a brood-chamber, so the question is open. In light of its southern distribution, encrusting habit, and characters typical of *Favosipora*, *Borgiola otagoensis* is here regarded as belonging to this austral genus.

The species was thoroughly described by the authors and is not redescribed here. In life, the colony colour is white. Colonies have been obtained from 38–104 m on the Otago shelf and from 31 m in eastern Foveaux Strait.

Figs 9–14. *Favosipora marmorosa* sp. nov. 9–10, NIWA Stn Z9684, Spirits Bay, profile (9) and frontal (10) views of two colonies showing distribution of pigmentation, $\times 3$. 11, NIWA Stn Z9701, Spirits Bay, showing size variations in white monticules, mostly kenozooids, separated by troughs of pigmented autozooids, $\times 6.5$. 12–14, NIWA Stn Z8664, off Whangaroa Harbour: 12, surface of colony showing parts of two brood-chambers, $\times 19$; 13, part of brood-chamber with oeciostome between larger zooidal apertures, $\times 148$; 14, zooidal apertures with edge of brood-chamber subjacent, $\times 338$.



Figs 16–18. *Favosipora rosea* sp. nov., NIWA holotype H-741, Otago Shelf: 16, surface of large colony showing brood-chamber with two oeciostomes (arrows), $\times 16$; 17, close-up of right-hand oeciostome, $\times 111$; 18, zooidal apertures with pinhead spinules (mural spines), $\times 116$.

***Favosipora rosea* sp. nov.**

(Figs 16–18)

Favosipora sp. nov.: Gordon 1996: 5, text-fig.*Favosipora* sp.: Weedon and Taylor 1996: 250, figs 1b, d, 6c–f.

Material examined. NIWA holotype H-741 from the Otago Shelf and paratype P-1212 from NIWA Stn B226.

Etymology. From the Latin, *roseus*, pertaining to roses, alluding to the pink to orange-pink colour of the colony.

Description. Colony adnate, large and mounded, up to 21 mm in longest dimension, with up to ~43 monticules. Small colonies not seen. Monticules variable in size and spacing, either somewhat circular, ~1.20–1.50 mm in diameter with centre-to-centre spacing of ~1.80–3.00 mm, or sometimes quite elongate, up to 3.64 mm long and 1.50 mm wide. Marginal lamina well developed.

Kenozooids and autozooids with polygonal outlines, frontally distinguishable by greater number of pinhead spinules (mural spines) visible on interior walls of kenozooids. Kenozooids 0.056–0.15 mm in internal diameter, smaller sizes commoner in monticules, generally of similar size to autozooids. Latter mostly ~0.13–0.15 mm in internal diameter between monticules, but often smaller (as small as 0.094 mm in internal diameter) in autozooids occurring in bundles within margins of brood-chambers. Autozooidal apertures opening at same level as kenozooids, and apertural corners of both zooidal types usually with short points.

Nanozooids absent.

Marginal lamina smooth, skeletal ultrastructure of imbricating platey crystal-lites.

Brood-chambers with very irregular outlines and usually quite extensive, attaining 4.8 mm in maximum length, although, with two oeciostomes sometimes present, two contiguous chambers can appear externally as one. Chamber roof penetrated by numerous autozooidal peristomes in connate groups of four or more and densely perforated by tiny pseudopores lacking spokes. Large colonies with up to three brood-chambers. Oeciostome smaller than adjacent autozooidal apertures, simple, circular, 0.058 mm in diameter, attached to edge of autozooidal cluster.

Ancestrula not seen.

Remarks. This species is known only from the Otago Shelf and Foveaux Strait, off the southeastern coast of South Island, where it occurs on molluscan shell gravel from 40 to 85 m in depth. It is instantly recognisable from its large, pinkish, mounded colonies with non-peristomate autozooids with apertures of similar diameter to the kenozooids. It is the only New Zealand *Favosipora* species with pinhead spinules, a character that it shares with the Northern Hemisphere species *F. holdsworthii*.

In life, the characteristic reddish pigmentation takes the form of numerous minute spots distributed evenly across the frontal membranes of the autozooids and kenozooids except for a barren central area corresponding with the atrial opening of the autozooids, and they are especially dense at distal growing edges. Brood-chambers are unpigmented, appearing as white areas in the pigmented colony surface. Autozooids have eight tentacles, their tips curved slightly outwards. The tentacle crown diameter is 0.26–0.28 mm, and its height 0.17–0.26 mm.

Macular autozooids have slightly oblique, truncate tentacle crowns.

***Favosipora tincta* sp. nov.**

(Figs 19–21)

Material examined. NIWA holotype H-742 from NIWA Stn Z8664 and paratype specimen NHM 1875.1.5.33 from New Zealand (locality unspecified), Sinclair Collection.

Etymology. From the Latin, *tinctus*, dyed, painted, alluding to its colour.

Description. Colony pale pink, simple, circular, and more or less radially symmetrical, with single macular centre. Colony centre occupied mostly by kenozooids with round outlines, but this arrangement disturbed by development of gonozooid occupying one side of central area. Holotype colony (fertile) 3.90 mm in diameter including narrow lamina; paratype colony (fertile) 2.78 mm in diameter.

Macular kenozooids relatively large, ~0.094–0.15 mm in apertural diameter; elsewhere generally variable, 0.055–0.15 mm in diameter, therefore mostly larger than autozooidal apertures. Autozooids connate or single, arranged in uniserial (sometimes partly biserial) radii up to 0.94 mm long (8 peristomes) or small clusters of 2 or 3, or quincuncially. Apertures mostly radially oval, ~0.075–0.13×0.055–0.57 mm in diameter, or occasionally circular with diameter of 0.056–0.096 mm, and rim even or slightly bicuspid or unicuspid. Opening occasionally with terminal closure plate, entire or with a few tiny perforations.

Nanozooids absent.

Marginal lamina and zooidal interiors smooth to sparsely granular.

Brood-chamber single, irregular in outline, excentric with respect to colony centre, with some lobes between autozooidal radii, 1.30 mm in maximum length, 0.51 mm in minimum width. Gymnocystal roof densely perforated by tiny pseudopores lacking radial spokes. Oeciostome adjacent to raised brood-chamber margin, circular or oval, slightly elevated and a little flared, smaller than autozooidal apertures, 0.075 mm in diameter (holotype) or 0.067×0.057 mm (paratype).

Ancestrula not seen.

Remarks. This species is known with certainty only from off Whangaroa Harbour, northeastern North Island, at 28 m depth. It closely resembles *F. candida* but is pale pink (the colour residing in the skeleton) instead of white and has an excentric brood-chamber with simple pseudopores, autozooids in radii, rounded macular kenozooids (instead of polygonal ones), and no nanozooids.

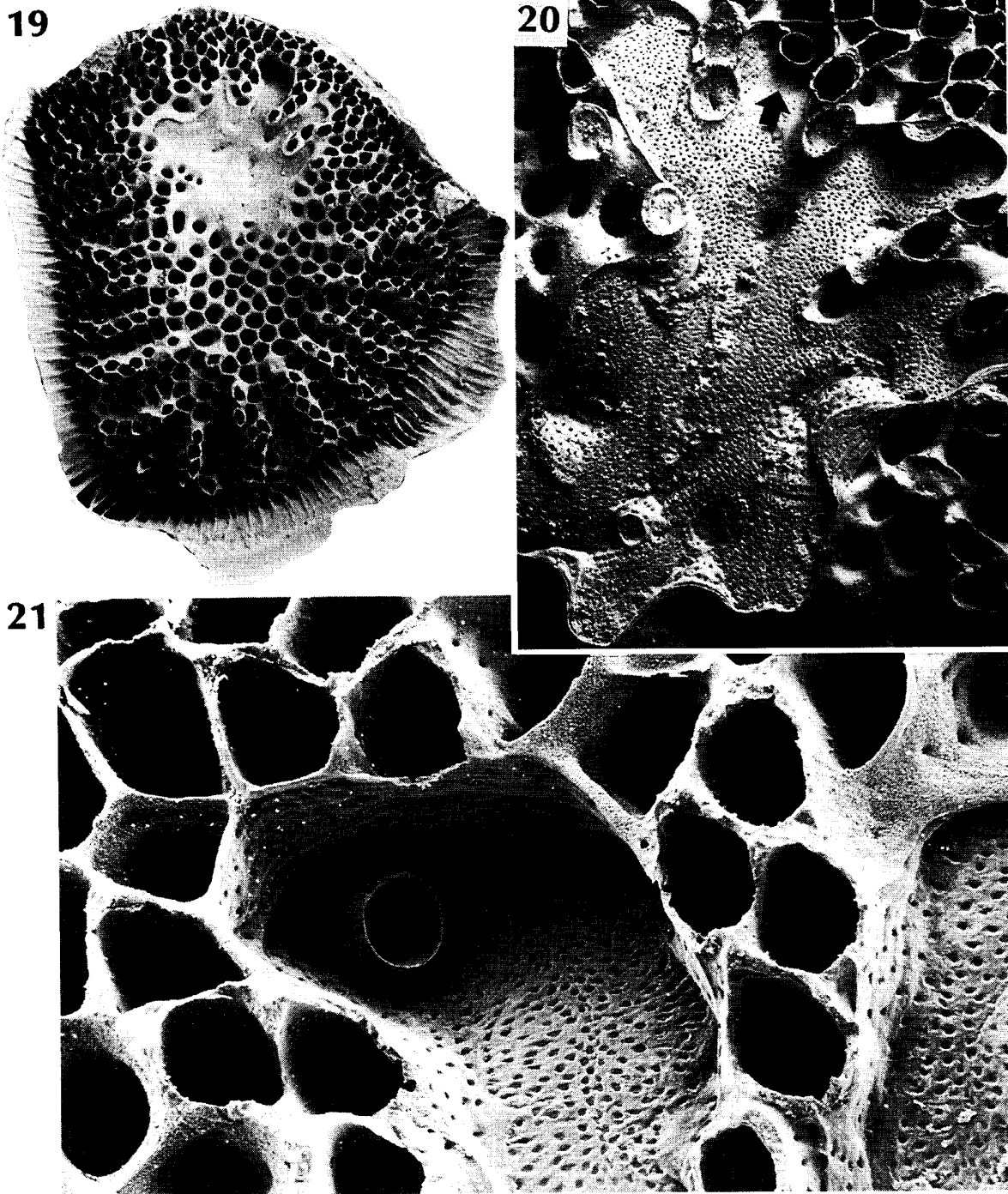
Family **Lichenoporidae** Smitt, 1867

Lichenoporidae Smitt, 1867: 405.

Disporellidae Borg, 1944: 249.

Genus ***Disporella*** Gray, 1848

Disporella Gray, 1848: 138.



Figs 19–21. *Favosipora tincta* sp. nov. 19 and 21, NIWA holotype H-742, Stn Z8664, off Whangaroa Harbour: 19, whole colony with brood-chamber, oeciostome visible in distalmost lobe, $\times 16$; 21, close-up of brood-chamber lobe with oeciostome, $\times 147$. 20, paratype NHM 1875.1.5.33, Sinclair Collection, New Zealand, brood-chamber, oeciostome arrowed, $\times 57$.

Heteroporella Busk, 1859: 126.

Orosopora Canu and Bassler, 1920: 822.

Type species. *Discopora hispida* Fleming, 1828: 530, by monotypy.

Revised diagnosis. Colony adnate; simple and radial, or compound and irregular. Autozooids arranged in radial series and/or quincuncially, separated by kenozooids. Peristomial apertures typically produced into one or more points, never wholly lacking these. Kenozooidal chambers sometimes becoming constricted by iris-like partitions or completely sealed by interior-walled diaphragms. Brood-chambers occupying macular centres, one or two per macula, with lobes extending radially between autozooids, oeciostomes typically opening at distal ends of lobes, not in centres of maculae; floor of brood-chamber comprising skeletal distinct layer, even if irregular, both floor and roof devoid of inwardly projecting mural spines. Skeletal ultrastructure predominantly of foliated crystallites, imbricated distally.

Remarks. There has been considerable confusion in the use of the genus names *Lichenopora* Defrance, 1823, introduced for fossil species, and *Disporella* Gray, 1848, introduced for Recent species. Gordon and Taylor (1997) reviewed the historical use of these names, pointing out that *Lichenopora* was not used for any Recent species until Smitt (1878a), and *Disporella* was not used for any fossil species until Brood (1972) (see Sabri 1988). The Eocene type species of *Lichenopora*, *L. turbinata* [designated by d'Orbigny (1853)], is shaped like a cone, and the genus concept originally included only conical-pedunculate forms. Michelin (1841–48) and Reuss (1846) expanded the generic concept (also based on the arrangement of autozooids) to include adnate forms and were apparently followed in this by Smitt (1878a, b), who in turn influenced Hincks (1880). This was unfortunate because it was unnecessary. Prior to Gray (1848), Recent adnate lichenoporids had generally been included in *Tubulipora*, a genus of fixed-walled cyclostomes. Gray (1848) introduced three new subgenera and one new genus for *Tubulipora* auctt.: subgenera *Patinella* (type species *Madrepora verrucaria* Fabricius, 1780), *Disporella* (type species *Discopora hispida* Fleming, 1828), and *Pencilletta* (type species *Tubipora penicillata* Fabricius, 1780), and genus *Phalangella* (type species *Tubulipora phalangea* Couch, 1844). Most of these names have not been used or have been overlooked. Following Gray, *Disporella* [or, as misspelled by Busk (1859, 1875), *Discoporella*] was used for living adnate lichenoporids until Smitt (1878a, b) and subsequent workers included them in *Lichenopora*. Borg (1944) reintroduced *Disporella* and even created a new family, Disporellidae, for the genus, claiming significant differences between adnate *Lichenopora* auctt. (i.e., *Patinella*) and *Disporella*. These were:

Lichenoporidae: kenozooids soon roofed over by porous calcified layer with secondary kenozooids above them; one early-forming central brood-chamber only, formed by fusion of kenozooids, and sometimes having lobes between autozooidal radii; vertical budding of subcolonies;

Disporellidae: kenozooids not roofed over but only partially closed by iris-like diaphragm; brood-chambers not developing early, formed by calcareous layer developing over kenozooids to form brood-chamber floor, restricted to interradian positions; lateral budding of subcolonies.

As Osburn (1953) and others have pointed out, some of these distinctions are

not clear-cut. Certainly in the species dealt with here, there are variations depending on colony size and age and, possibly, non-genetic environmental factors (such as initiation and onset of gametogenesis and embryogenesis in relation to growth rate and size). For example, in *Disporella novaehollandiae*, iris-like kenozooidal diaphragms are not seen in every colony, but seem to develop in macular centres in which brood-chambers are late to develop. Brood-chambers may develop very early, judging from some quite small colonies in which they are found, whereas some other colonies may attain a significant size, even budding subcolonies, yet still lack externally visible brood-chambers. Further, in the species described here, brood-chambers are generally associated with macular centres. Canu and Bassler (1920) introduced *Orosopora* (type species *Discoporella ciliata* Busk, 1875) for species in which (“the ovicell is placed near the zoarial margin and not at the centre of the zoarium”), based on an illustration of Waters (1889). If Waters’s (1889) identification was correct, this arrangement is not only exceptional for *D. ciliata* [i.e., *D. pristis* (MacGillivray, 1884), see below], but for lichenoporids generally, although it accords with Borg’s (1944) concept of *Disporella*. Notwithstanding these difficulties, it seems possible to discriminate between *Patinella* (adnate Recent *Lichenopora* auctt.) and *Disporella* on the basis of brood-chamber formation and the appearance of the brood-chamber interior. Using thin sections, SEMs, and drawings, Schäfer (1991, figs 65–71, pls 39–45) illustrated the appearance of the floor and roof of the brood-chamber at different developmental stages in *Patinella verrucaria*, *P. radiata* (Audouin, 1826), and *Disporella hispida*. There is a distinct floor in the last species, formed by a layer of calcification that spreads over an area of kenozooids; in *Patinella* there is no consistent floor, only an irregular area of low rims of partly resorbed kenozooids. The underside of the brood-chamber roof appears similar, whereas in *Disporella* it is relatively smooth.

One other adnate Recent genus may possibly be discriminated, viz. *Doliocoitis* Buge and Tillier, 1977, established for *D. atlantica*, a thickly encrusting to nodular species that Buge and Tillier (1977) attributed to the Cerioporina. In fact, although the zooids lack peristomes and apertural processes, the species is a typical lichenoporid with a ramifying, interior-walled brood-chamber. The brood-chamber has a discrete floor, as in *Disporella*, but the roof does not develop surface reticulations and gives the appearance of becoming relatively rapidly overgrown by zooids.

The precise identity of *Disporella hispida*, the type species of *Disporella*, needs clarifying and stabilising. As Alvarez (1992) recognised, Hayward and Ryland (1985) illustrated at least two species under the name of *D. hispida* in their synopsis of the British fauna. In the absence of any Fleming material, Alvarez (1992: 209) selected a neotype (NHM 1899.7.1.4187). However, in our opinion, there are two main problems with Alvarez’s choice:

- 1) The neotype is not topotypic. The nominal locality of the neotype is “Tenby (?)”, Wales, whereas Fleming’s specimens came from the Shetland Islands—“This species is very common in Zetland, adhering to *Cellepora cervicornis* [= *Porella compressa*]” (Fleming 1828: 530).

- 2) The neotype does not conform to the original description. Fleming (1828) described *D. hispida* thus: “the cells [zooids] distributed or radiated, with denticulated orifices”; “Breadth nearly an inch [i.e., 2.5 cm]; hispid, the cells [zooids] seem distributed over the whole surface..... there are, however, waved porous grooves and the cells seem disposed on each side of these in irregular transverse rows,

united or free, short, with expanding orifices, dividing into irregular spinous processes." This does not correspond with Alvarez's neotype, which cannot be described as "hispid", nor are the orifices "expanded", although they may have short, inconspicuous projections. We agree with Alvarez (1992) that his neotype specimen is conspecific with *Lichenopora mamillata* Lagaiij, 1952 (see also Sabri 1988: 150); we further suggest, 1) that it may possibly be attributable to *Doliocoitis* on the basis of the brood-chamber, and 2) the correspondence of genuine *D. hispida* to fig. 46A, B of Hayward and Ryland (1985) [attributed by Alvarez to *Disporella smitti* (Calvet, 1906)] and possibly also to their fig. 45A–F (?=*D. robusta* Alvarez, 1992). Possibly supporting our view is the likelihood that *Discopora meandrina* Peach, 1878 is a junior synonym of *D. hispida*. Peach's specimen (apparently no longer extant in the collections of the NHM), also came from the Shetlands, attached to *Porella compressa*. Peach's illustrations (1878, pl. 23, figs 6–8) show a compound colony and distinct peristomial apertural spikes. Although Peach described these as single ("never bifid or trifid"), this character is usually variable, based on colonies we have seen. Peach considered his species as quite distinct from Fleming's—"nor are the pores at the bottom stellate as in *D. hispida*"; Hincks (1880: 474–475) refers to the pores as "ostioles", i.e., kenozooids. Inasmuch as *D. hispida* has no stellate kenozooids, Peach may have been mistaken in his understanding of *D. hispida*. Fleming (1828) also wrote, concerning the appearance of the colony, "the figure of Cordiner is a tolerably accurate representation." Cordiner (1794) published a plate labelled "Peacock's Feather Coralline, &c.", illustrating an erect, branching scleractinian coral and some encrusting bryozoans including a lichenopod. The latter, somewhat calyciform, had autozooids with five well-developed apertural spines (cf. Hayward and Ryland 1985, fig. 45A).

***Disporella pristis* (MacGillivray, 1884)**

(Figs 22–30)

Discoporella hispida: Hutton 1873: 104. [Not Fleming, 1828, erroneously attributed to Johnston]

Discoporella ciliata Busk, 1875: 31, pl. 30, fig. 6, pl. 33, fig. 4; Hutton 1877: 361; 1880: 199; Haswell 1880: 354. [Preoccupied]

Discoporella pristis MacGillivray, 1884: 126, figs 3, 3a, b; 1887: 219.

Discoporella echinata MacGillivray, 1884: 127, figs 4, 4a; 1887: 219.

Lichenopora ciliata: Waters 1887a: 263, pl. 7, fig. 5; 1889: 283; Jelly 1889: 134; Philipps 1900: 441.

Lichenopora hispida: Waters 1887b: 345; Hamilton 1898: 197; Fleming 1971: 9. [Not Fleming, 1828]

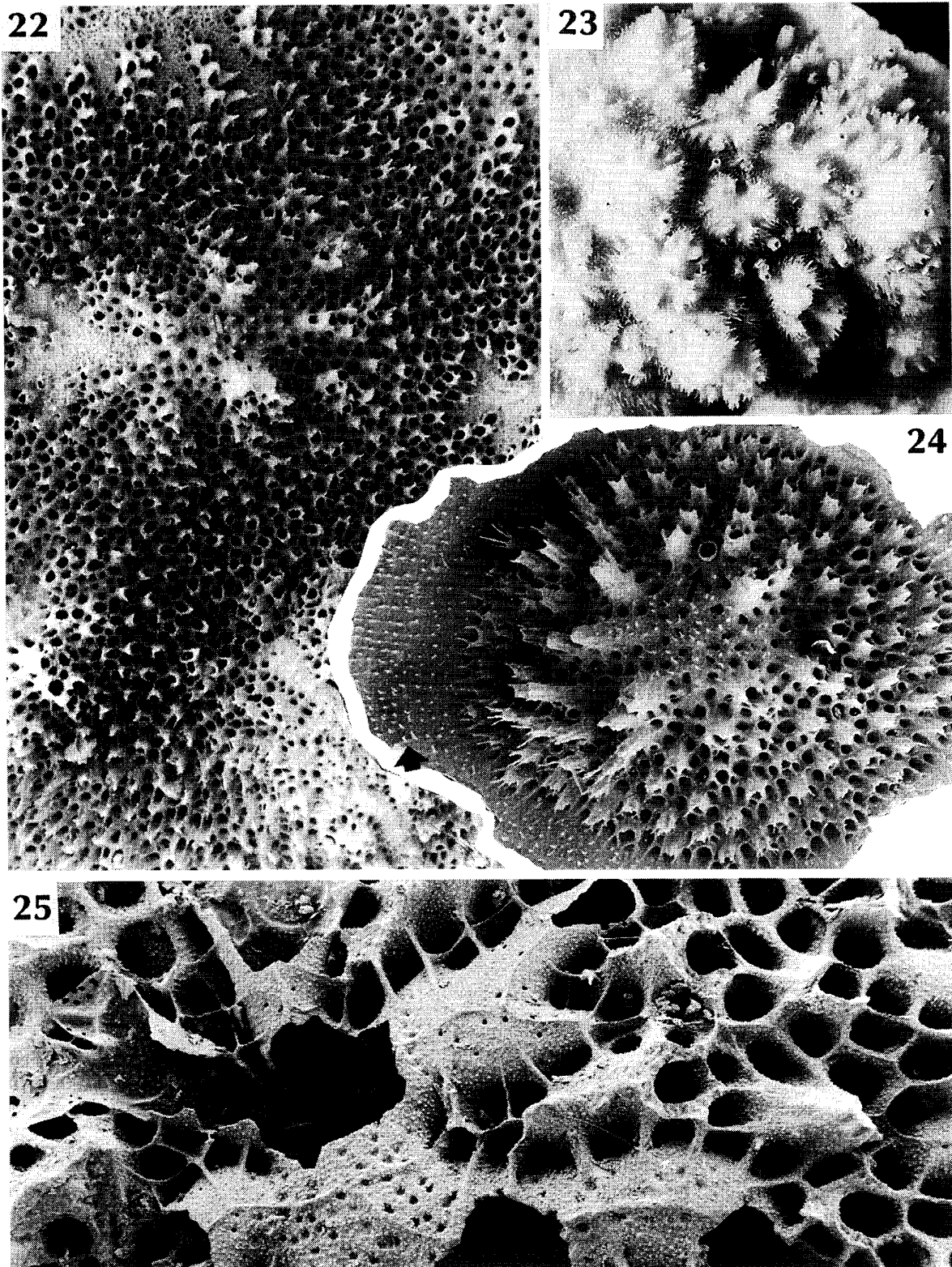
Lichenopora echinata: Waters 1889: 282, pl. 15, figs 2, 3, 6; Jelly 1889: 134.

Lichenopora pristis: Jelly 1889: 137; Hamilton 1898: 197; Hutton 1904: 299; Sabri 1988: 159.

Lichenopora holdsworthii: Hutton 1891: 107; 1904: 299. [Not Busk]

Lichenopora buski Harmer, 1915: 161, pl. 12, figs 4, 5; Okada 1917: 354; not Canu and Bassler 1928: 163, pl. 29, fig. 9; Canu and Bassler 1929: 558, pl. 88, figs 7–10; ?Mawatari 1952: 262; ?1955: 50; ?Mawatari and Mawatari 1974: 354, pl. 30, fig. 2.

Syn. nov.



Figs 22–25. *Disporella pristis* (MacGillivray, 1884). 22, NIWA Stn Z8664, off Whangaroa Harbour, part of large compound colony, $\times 13$; 23, NIWA Stn Z9684, Spirits Bay, part of large compound colony, with numerous cylindrical polychaete tubes protruding, $\times 3.8$; 24, NIWA Stn B490, Dusky Sound, small fertile colony (oeciostome arrowed) displaying thorn-like processes on marginal lamina, especially at left (arrowhead), $\times 15$; 25, NIWA Stn Z8639, Cavalli Islands, part of developing brood-chamber, $\times 72$.

Orosopora ciliata: Canu and Bassler 1920: 822.

Disporella buski: Borg 1944: 227; Brood 1976: 299, fig. 17D–G; Buge, 1979: 243, pl. 9, fig. 1; Alvarez 1992: 238, fig. 18A–C; Hayward and Ryland 1995: 534, fig. 2B–D.

Disporella echinata: Borg 1944: 229.

Disporella pristis: Borg 1944: 232.

Disporella buskii [sic]: Fleming 1971: 9.

Disporella fimbriata: Gordon and Ballantine 1977: 124. [Not Busk]

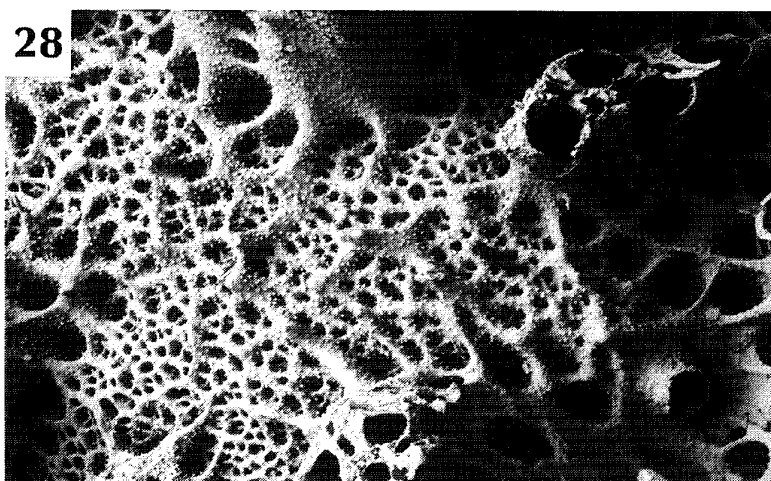
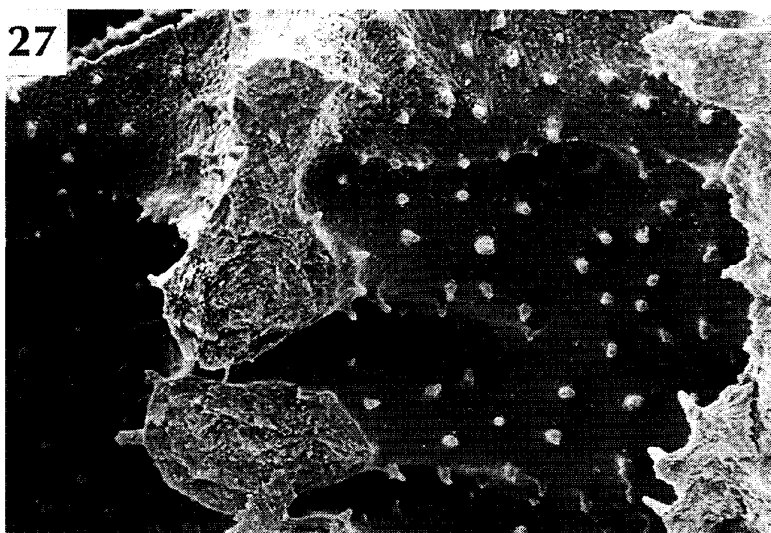
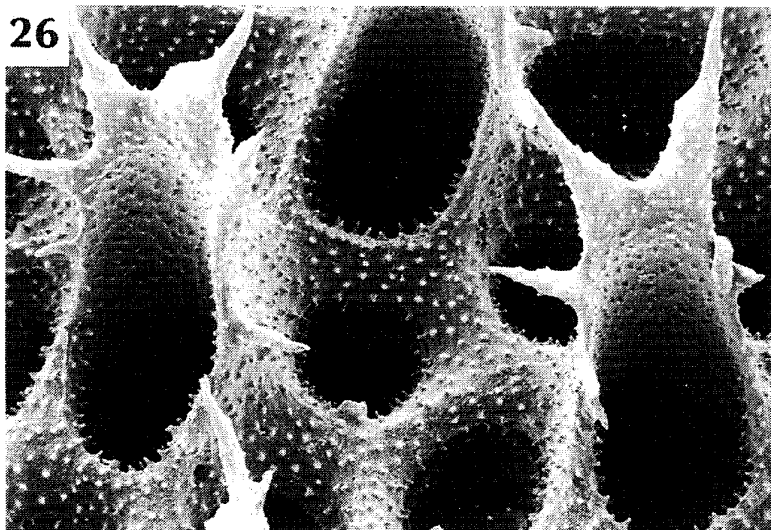
Disporella gordonii Taylor, Schembri and Cook, 1989: 1071, figs 3B–D, 6A–F; Taylor 1991: 488, pl. 1, figs 2–8; 1994: 165, fig. 16C; Taylor *et al.* 1995: 206, figs 1c–f, 2a–c, 3a, b, 4a–f, 5e. **Syn. nov.**

Material examined. NHM: holotype of *Discoporella ciliata*, 1899.7.1.519, Recent, Cape of Good Hope; *Discoporella pristis*, J. B. Wilson/MacGillivray Collection, 1897.5.1.1166, Recent, Australia; *Discoporella echinata*, J. B. Wilson/MacGillivray Collection, 1897.5.1.1162, Recent, Australia; holotype of *Disporella gordonii*, 1988.3.1.541, Recent, Otago Shelf; paratypes of *D. gordonii*, 1988.3.1.2–7, 17, 18, 21, 30, 51, 62, 63, 106, 263, 276, 295, 319, 363, 364, 373, 387, 389, 304, 400, 406–8, 465, 467, 499. NIWA: NIWA Stns B473, D273, E821, K801, H57, M779, Z8639, Z9976; D. P. Gordon collection, Goat Island Bay, Leigh, Chatham Islands.

Description. Colony whitish/ivory-coloured, simple, circular, and radially symmetrical, or subcircular to oval, with single macular centre, to compound, irregular, with scores of maculae (to more than 100, assuming only one colony involved). Maculae very variable in size and spacing, not only within colonies but particularly between “young” compound colonies and old, thick, multilamellar colonies. In simple colonies, central area of macula between opposing radii generally 0.75–1.32 mm in diameter (attaining 0.56×3.21 mm in one colony with elongate-oval macula); in compound colonies, entire maculae (central area plus radii) generally ranging from 2.30 to 3.02 mm in diameter, with adjacent centres 2.83–3.87 mm apart; in thick multilamellar colonies (whether symbiotic with hermit crabs or not), maculae often becoming thick (up to 4 mm high) with perpendicular zooidal tubes. Completely adnate, with entire basal surface affixed to substratum or, where substratum irregular or limited, basal wall curving upwards at edges. In profile, small infertile colonies with slightly elevated central region surrounded by gently sloping zone of erect, fimbriate, autozooidal tubes slanted away from centre. With increasing diameter and height, lateral profile becoming steeper and autozooidal tubes approaching perpendicular. Entire colony surrounded by thin marginal lamina. Simple colonies up to 7 mm in diameter, including lamina; large, compound colonies up to 6 cm long or longer when constructing tubes occupied by hermit crabs.

Centre of neanic colonies a few millimetres in diameter showing proximal

Figs 26–30. *Disporella pristis* (MacGillivray, 1884). 26–27, NIWA Stn Z8664, off Whangaroa Harbour: 26, zooidal apertures near colony margin, displaying arrangement of peristomial processes, ×161; 27, autozooidal interior, apertural rim at top, ×454. 28, NIWA Stn Q686, Cook Strait, reticulate surficial calcification of ‘old’ brood-chamber, oeciostome at lower right, ×59. 29, NIWA Stn B490, Dusky Sound, close-up of part of marginal lamina of colony in fig. 24, showing lines of thorn-like processes and tiny pustules, ×211. 30, NIWA Stn K801, Raoul Island, attenuated peristomial processes from protected part of colony margin, ×102.



ends of recumbent autozooids, between and over which kenozooids develop. Kenozooids also between short autozooidal radii and around free autozooidal peristomes of smaller diameter. At first, kenozooids relatively thin walled, but lumen diameter soon reducing because of wall thickening. Kenozooidal wall thickness variable, however, and, even at growing edge where kenozooids and autozooids differentiating, can be surprisingly thick. Entire exterior and interior surface of kenozooids densely granular and covered with sparsely distributed, needle-like spinelets.

Autozooids variably disposed; most commonly in short radii of bi-, tri-, or quadriserial, connate or near-connate peristomes near colony/macula centre; between radii and periphery all peristomes quincuncial. In some simple, neanic colonies, however, all autozooids quincuncial. In older, simple colonies and most compound colonies, proximal ends of radii comprising small groupings of 3–4 autozooids, each thicker-walled on macular side of peristome than abmacular; vertical rows of pores on lateral faces between fused peristomes. Peristomes sometimes continuing outwards as short connate rays, uni- to quadriserial; some rays with up to 14 autozooids in series. Apertural diameter of autozooids 0.069–0.109 mm at growing edge, 0.069–0.135 mm in radius (maximum and minimum diameters reflecting oval shape of many peristomial lumina). Peristomes consistently elongated on macular side into 1–3 points; 2–3 additional points often developing at sides of aperture. All surfaces of autozooids densely granular, often also with sparse spinelets.

Marginal lamina densely and evenly granular; at high magnification granules appearing pustule- or even tubercle-like. Radial septa indicating vertical walls of future zooids generally absent, but one colony from NIWA Stn B490 with parallel rows of spinules (Figs 24, 29). Surrounding skeletal ultrastructure of imbricating platey crystallites.

Brood-chamber developing in macula centre, initially porous but surface soon becoming covered with fine and coarse reticulate calcification. Lobes of brood-chamber not extending far between autozooidal radii. One, rarely two oeciostomes per macula, each located at distal end of short lobe, facing frontally or laterofrontally, either circular or slightly compressed transversely or longitudinally; oeciostome thin-walled, simple, usually slightly granulated, not flared but sometimes slightly recumbent on macular side, giving appearance of sloping ledge there; diameter variable depending on size and age of colony, generally 0.096–0.135 mm in external diameter, but one oval oeciostome extending 0.221 mm in long axis.

Ancestrula not seen.

Remarks. In the New Zealand region, *D. pristis* is distributed from Raoul Island in the Kermadec group to the Auckland Islands Shelf. It is common around mainland New Zealand from Spirits Bay along both coasts through Cook Strait to the Chatham Islands, Fiordland, and Foveaux Strait, from the low intertidal to 305 m depth on a range of substrata. Its wider distribution appears to include much of the Indo-Pacific from Japan through Indonesia, the Great Barrier Reef, southern Australia, and East and South Africa.

Busk's (1875) name for this species was *Discoporella ciliata*. The epithet was unfortunate since he had already (Busk 1855) used the binomen *Discopora ciliata* Busk, 1855 for another lichenopoid (unillustrated) that, according to Harmer (1915), was a junior synonym of *Madrepora verrucaria*. Jelly (1889) synonymised

Busk's two species, using the combination *Lichenopora ciliata*; Harmer (1915) introduced a replacement name, *L. buski*.

According to Busk (1875: 31), *Discoporella ciliata* was found at the Cape of Good Hope ("on *Retepora*") and New Zealand ("on *Hornera*"). Harmer (1915) included in his synonymy putative records from Queensland (Haswell 1880), New South Wales (Waters 1887a), and the Loyalty Islands (Philipps 1900), and he also included museum specimens from the Torres Strait and Japan in his account, mentioning the fine granularity of the marginal lamina in the former and fine internal "denticulation" of kenozooids in the latter. Hayward and Ryland (1995) illustrated by SEM a fertile colony from Heron Island, Great Barrier Reef; we consider this conspecific with our New Zealand material, since it accords in the characters (including size) of the autozooidal peristomes, brood-chamber, and oeciostome, and in the distinctive granularity of all surfaces, especially the marginal lamina.

Alvarez (1992) illustrated by SEM the infertile holotype specimen of *D. ciliata* from the Cape of Good Hope and we have also reexamined it. The specimen shares the same distinctive granularity of all surfaces, sparsely distributed spinelets, and fimbriated peristomial apertures as our New Zealand material. It differs most strikingly in the thinness of the zooidal walls at the growing edge, but a colony from Goat Island Bay, New Zealand, and the specimen of Hayward and Ryland (1995) from Heron Island show similar wall thickness. Unfortunately, despite the studies of Hayward and Cook (1979, 1983), the bryozoan fauna of southern Africa is still poorly known, especially the cyclostomes—they did not encounter the species, and neither did Day (1969). Brood's (1976) SEM illustrations of *D. buski* from Kenya, however, accord with the New Zealand material, leading us to accept provisionally the wide Indo-Pacific distribution. Given the short-lived larval dispersal phase of cyclostomes, this distribution demands evaluation using molecular techniques.

Disporella gordonii Taylor, Schembri and Cook, 1989 was based on large, heli-cospiral, compound colonies symbiotic with hermit crabs. Such robust multilamel-lar colonies, lacking a well-developed marginal lamina at the actively growing tube aperture, are superficially very distinctive compared to young, simple colonies. Comparison of a large sample of small, simple and large, compound colonies, both symbiotic and non-symbiotic, from throughout New Zealand shows that all of these specimens share the same fundamental characters, and *D. gordonii* is therefore placed in synonymy with *D. pristis*.

New Zealand specimens have also been attributed to *D. hispida* (e.g., Hutton 1873; Hamilton 1898), and indeed there are many similarities in the form of the colony, peristomial processes, and brood-chambers. One consistent difference is the oeciostome, which is always internally smooth-surfaced in *D. hispida* and covered by tiny mural spines in *D. pristis*.

Waters (1889) examined southern Australian lichenoporids and noted great similarities among *D. pristis* (MacGillivray), *D. echinata* (MacGillivray), and *D. fimbriata* auctt. (not Busk). He concluded that the latter two species were synonymous and that it was probable that *D. echinata* and *D. pristis* were merely simple and compound colonies of the same species. Borg (1944) agreed that it was an open question. MacGillivray's (1884) descriptions and illustrations are very suggestive of close relationships, and our examination of J. B. Wilson/MacGillivray material in the NHM persuades us that we are dealing with one widespread species. *Dis-*

porella pristis has page priority over *D. echinata* in MacGillivray (1884); therefore, acting as first revisers, we choose the former name as valid.

Disporella wanganuiensis (Waters, 1887)
(Figs 31–36)

?*Discoporella porosa* Haswell, 1880: 354.

Lichenopora wanganuiensis Waters, 1887b: 346, text-fig.; Hamilton 1898: 197; Fleming 1971: 9.

?*Lichenopora mediterranea*: Harmer 1915: 164, pl. 12, fig. 3; ?Okada 1917: 354; Canu and Bassler 1929: 561, pl. 90, figs 1–3; ?Mawatari 1955: 50; ?Mawatari and Mawatari 1974: 355, pl. 30, fig. 3; ?Mawatari 1986: 80, fig. 15. [Not de Blainville]

?*Disporella sibogae* Borg, 1944: 226, 232; Brood 1976: 299, fig. 17H, I [not fig. 17A–C, = *D. novaehollandiae*]; Winston 1986: 30.

Material examined. Numerous colonies from NIWA Stns E820, E821, G259, Y38. Fossil: NHM BZ4861, Pliocene, Nukumaruan, Nukumarua Limestone, Nukumarua, Wanganui, New Zealand.

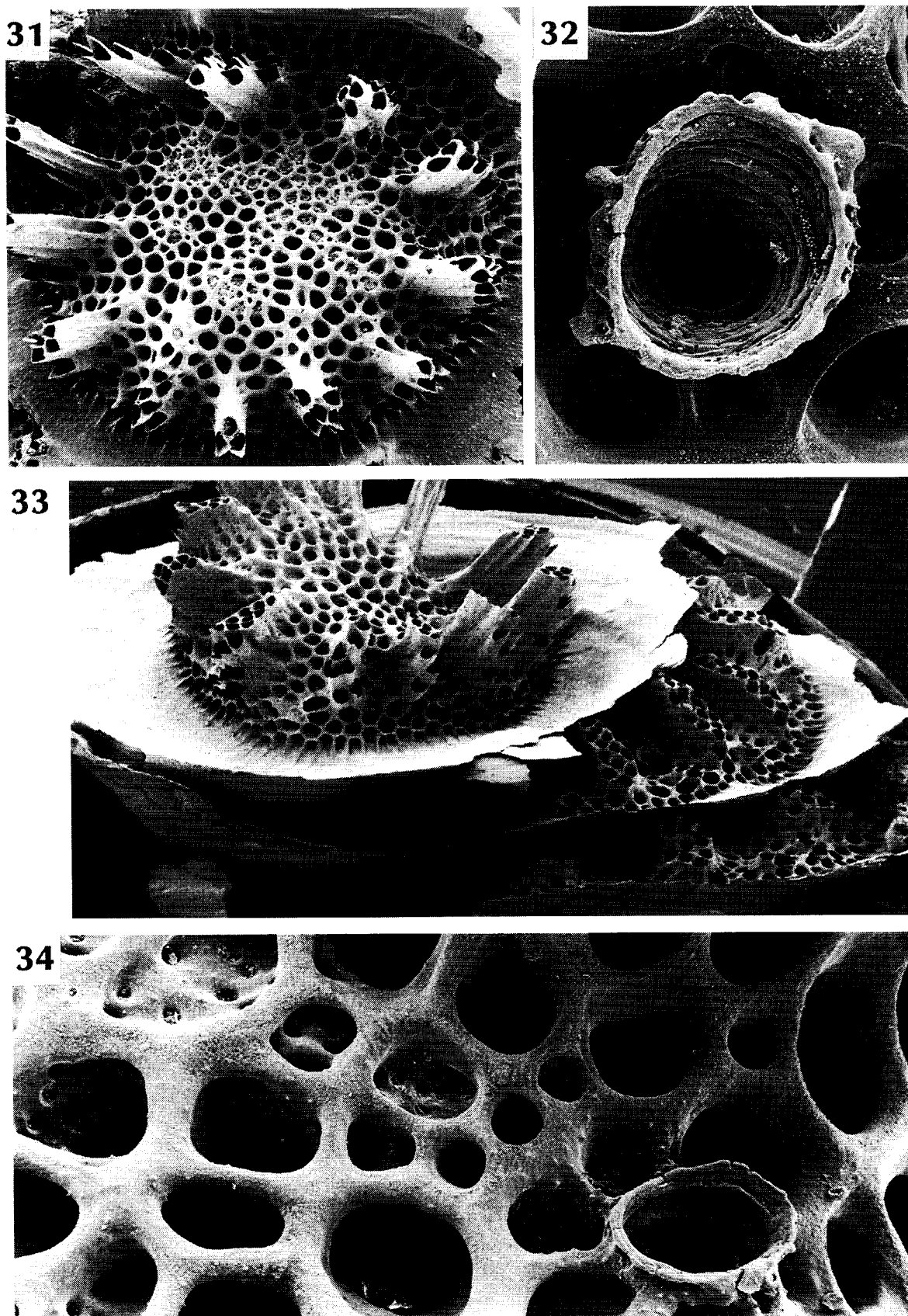
Description. Colony pink, simple, circular, and mostly radially symmetrical, with single macular centre; or vertically compound, with up to three smaller sub-colonies above parent colony. Maximum diameter 7 mm including marginal lamina. Macular centre between opposing radii 0.18–0.25 mm in diameter in mature (brooding) colonies. Completely adnate, with entire basal surface affixed to substratum except where outgrowing it. In profile, colonies with centrally depressed region surrounded by zone of relatively steeply sloping, erect, radiating autozooidal tubes; tubes adjacent to colony centre near vertical or slightly slanted away from centre.

Surface of depressed colony centre comprising layer of relatively short, alveolar kenozooids with polygonal outlines and relatively thin walls. Identical kenozooids also developed in interradii between autozooidal rows, evidently not becoming further subdivided internally. Inner skeletal surface of kenozooids smooth, with no spinules or tuberculations.

Autozooids connate, in radiating rows 1–3 zooids wide; proximal (macular) ends of radii sometimes fascicle-like, occasionally with only one zooidal peristome. Largest colonies with up to 19 primary radii facing macula centre, and fewer, shorter, secondary radii towards colony margin; radii highest (up to 1.22 mm) close to macula. Primary radii in mature colonies 0.56–1.67 mm long, interradii spacing 0.32–0.53 mm. Autozooidal peristomial openings typically radially ovate, 0.12–0.17 mm long and 0.094–0.12 mm wide; apertural diameters at growing margin 0.13–0.15 mm. Shape of peristomial opening simple or mitriform, not fimbriated. Outer faces of autozooids with pseudopores.

Marginal lamina almost smooth, with sparse minute granules; ultrastructure

Figs 31–34. *Disporella wanganuiensis* (Waters, 1887). 31–32, NIWA Stn G259: 31, simple colony with brood-chamber, oeciostome at middle right between autozooidal radii, $\times 17$; 32, oeciostome, frontal view, $\times 141$. 33, NIWA Stn E821, Puysegur Ridge, vertically compound colony, $\times 13$. 34, NIWA Stn G259, brood-chamber lobe and oeciostome, $\times 130$.



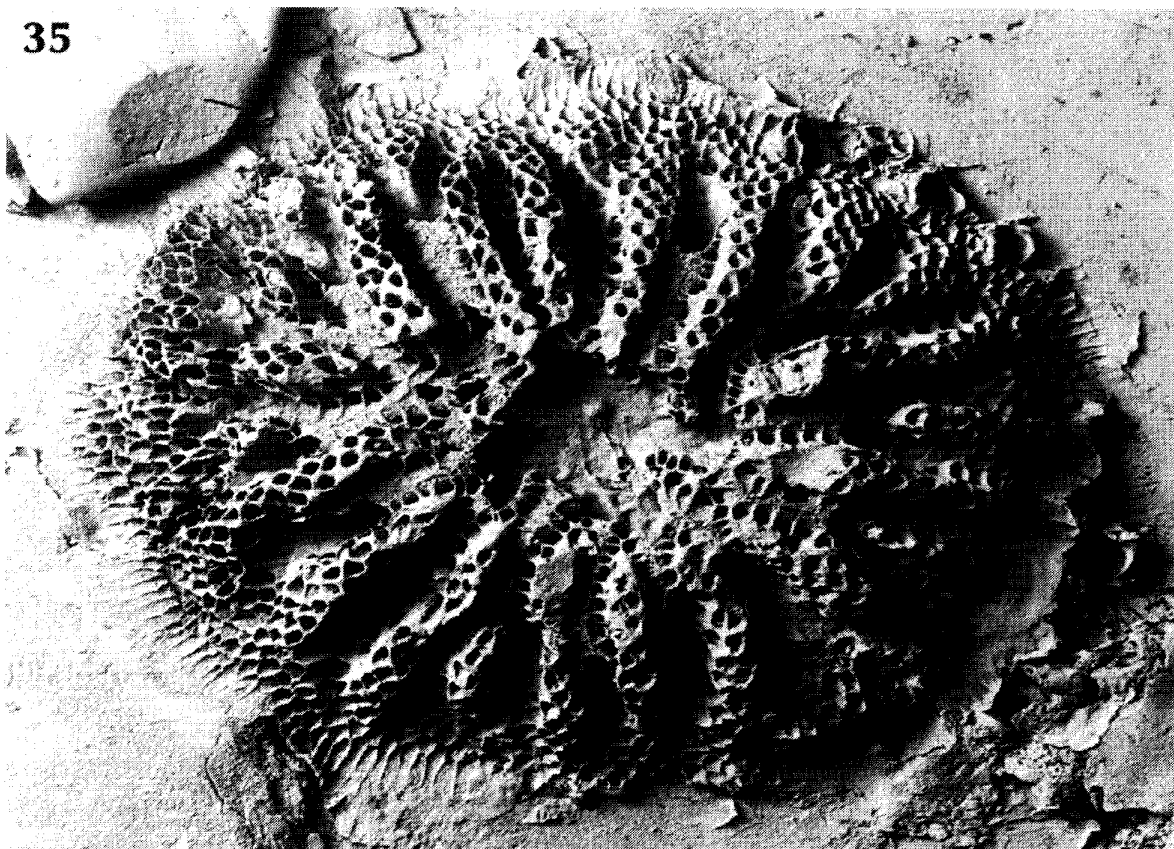


Fig. 35. *Disporella wanganuiensis* (Waters, 1887), NHM BZ4861, Pliocene, Nukumaru Limestone, Nukumaru, near Wanganui, fossil topotype colony with brood-chamber(s) deroofed centrally and extending between autozooidal radii, $\times 21$.

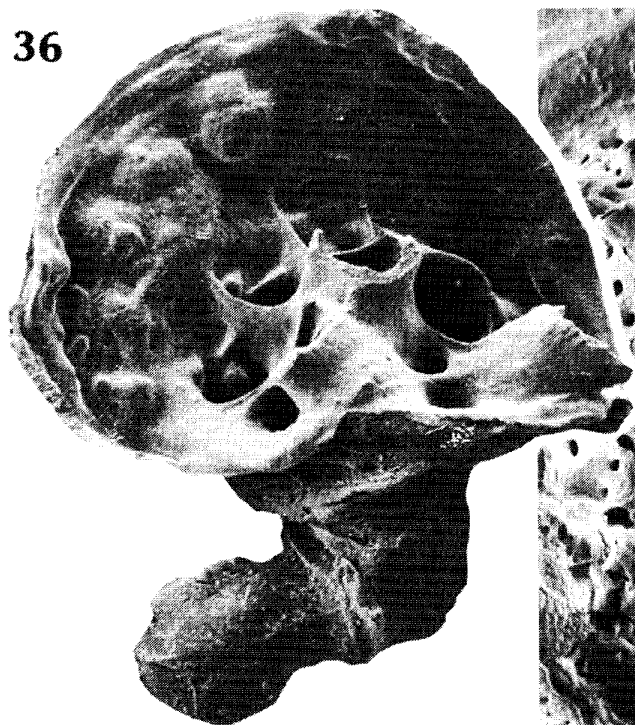
of imbricating platey crystallites.

Brood-chambers found in macula centres; either 1) single, nearly stellate, not occupying entire macula centre, with often only one interradiial lobe; oeciostome distal, opening between pair of radii about half-way towards colony margin; or 2) two or three more brood-chambers, each with its oeciostome, latter occasionally opening at end of very short lobe adjacent to macula centre. Oeciostome distinctive at high magnification: typically slightly radially oval, flared, made up of vertically concentric, minutely pitted and porous layers, and at bottom possessing subcircular opening surrounded by flange; external diameter of oeciostome ca. 0.15 mm or, if oval, up to 0.18 \times 0.24 mm. Brood-chamber roof surfaced by lacelike tracery of kenozooidal walls, with minute pseudopores, these latter sunken and almost completely sealed by very fine radial spokes.

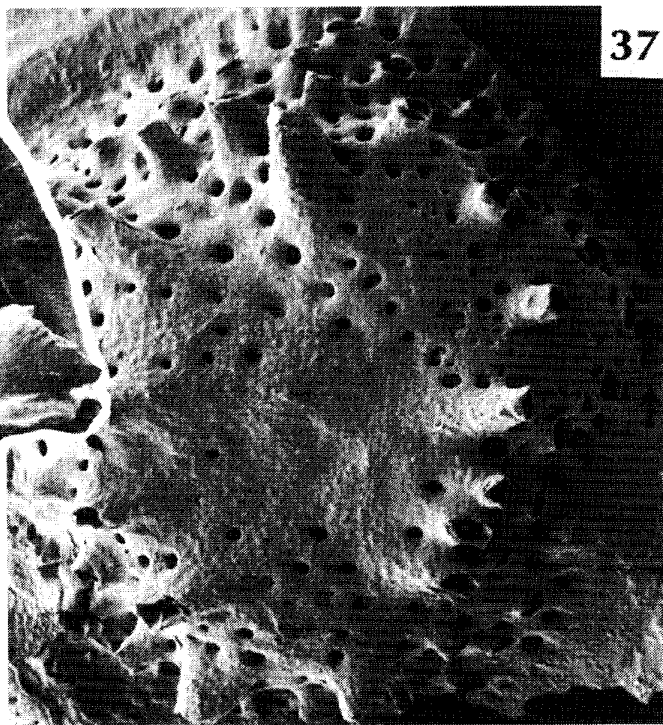
Fig. 36. *Disporella wanganuiensis* (Waters, 1887), NIWA Stn G259, Chatham Rise, ancestrula and earliest daughter zooids, $\times 93$.

Figs 37–39. *Disporella humilis* sp. nov., NIWA holotype H-743, Stn Y38, Puysegur Bank: 37, fertile holotype colony, brood-chamber represented by porous area at upper right, oeciostome visibly protruding at middle right (arrow), $\times 39$; 38, close-up of brood-chamber and oeciostome (arrow), $\times 143$; 39, pores in brood-chamber roof, $\times 1042$.

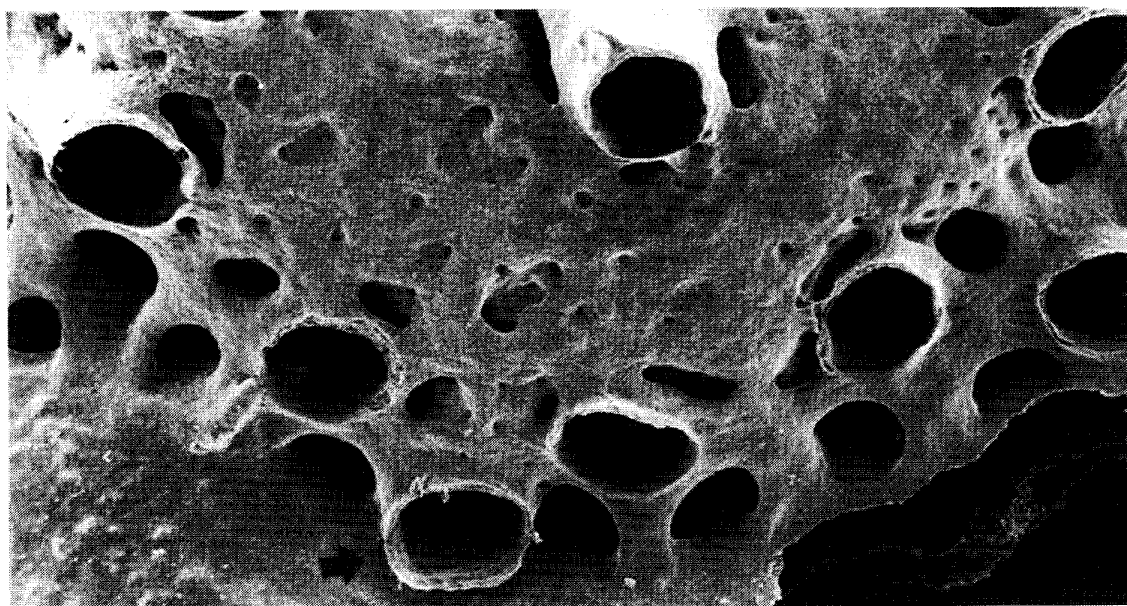
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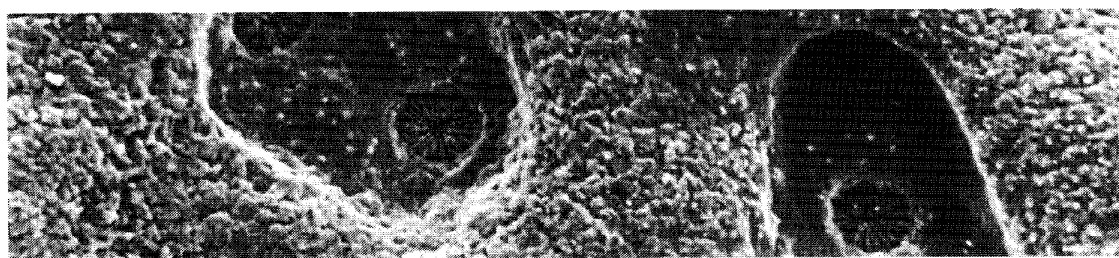
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38



39



Ancestrula with discrete, smooth-walled protoecium 0.15–0.20 mm wide, producing daughter zooids and frontally developing lamina rim almost immediately to form tiny, flabellate colony; distal tube straight or curved.

Remarks. In New Zealand, *Disporella wanganuiensis* is strictly a shelf species, found from 107 to 305 m depth on Puysegur Bank southwest of South Island and at 419 m depth on the Chatham Rise, typically on calcareous substrata including cidaroid spines. Distinctive features include the pink colour (retained in the skeleton), tall radii of connate peristomes, vertical stacking of subcolonies, and the layered construction of the oeciostome. One colony has a broken brood-chamber roof, allowing a distinct floor to be seen, typical of *Disporella*.

Owing to the poor quality of historic descriptions and illustrations (if present), it is not possible to be certain of the synonymy given above. Harmer's (1915, pl. 12, fig. 3) illustration of a whole colony of putative *Lichenopora mediterranea* de Blainville, 1834 from Indonesia closely resembles New Zealand colonies described here, but Harmer also described and illustrated pinhead spinules, which are lacking in the present material. Borg (1944) introduced a new name, *Disporella sibogae* Borg, 1944 for Harmer's specimens, citing *L. mediterranea* sensu Canu and Bassler (1929, pl. 90, figs 1–3) as a likely synonym. This appears extremely likely—Canu and Bassler (1929: 562) mention “very salient and biserial fascicles and the large polygonal cancelli with thin walls” and that the colonies “become superimposed rather easily”, which is in accord with the New Zealand specimens. Puzzlingly, however, neither Canu and Bassler (1929) nor Borg (1944) discussed Harmer's mention of pinhead spinules. Brood (1976) illustrated by SEM (but did not describe) a specimen from East Africa attributed to *D. sibogae*, which appears nearly identical with the New Zealand colonies. It, too, lacks pinhead spinules; there is also an adjacent, laterally budded subcolony, which is not usual (unless the specimen comprised two genetically identical colonies that had fused laterally). Harmer (1915) suggested that *Lichenopora wanganuiensis* might be conspecific with the Indonesian specimens. Waters's species name is used here. He described and illustrated an infertile specimen with colonial and autozooidal dimensions that are in accord with the present New Zealand material. Study of comparative, fertile colonies (Fig. 35) from the Pliocene and Pleistocene close to the type locality of Wanganui supports this identification. Both Harmer (1915) and Borg (1944) suggested *Disporella porosa* Haswell, 1880 might also be synonymous with the Indonesian material. Haswell's poor description could certainly apply to the New Zealand material but he gave no illustration or dimensions. None of the above-mentioned authors mentioned colony colour.

Sabri's (1988: 113) attribution of *Lichenopora mediterranea* sensu Canu and Bassler (1929) and *D. sibogae* to “*Lichenopora stellata* (Reuss, 1847)” appears utterly confused [see also the discussion on page 114 of Sabri (1988)].

***Disporella humilis* sp. nov.**

(Figs 37–39)

Material examined. NIWA holotype H-742 from NIWA Stn Y38.

Etymology. Latin *humilis*, humble, alluding to the diminutive size of the species.

Description. Colony simple, circular, and mostly radially symmetrical, with single macula. Maximum diameter 2.5 mm including marginal lamina, 2.0 mm excluding lamina. Macula centre between opposing radii somewhat ovoid, 0.96×0.66 mm in diameter. Completely adnate, with entire basal surface affixed to substratum except where limited. In profile, colonies somewhat hat-shaped, with macula centre highest and somewhat flat, and sides vertical with autozooidal peristomes opening laterally. Surface of macula centre mostly imperforate, faintly granular-textured, with small kenozooidal openings towards periphery adjacent to autozooidal peristomes.

Autozooids quincuncial, projecting only 1–3 peristome widths beyond colony surface. Autozooidal apertures more or less circular near colony margin, 0.075 mm in diameter, becoming ovate near macula centre, 0.10 mm long and 0.066–0.075 mm wide; adjacent kenozooidal openings only 0.038 mm in diameter. Peristomial aperture simple, even, not projecting or fimbriated.

Marginal lamina smooth, its ultrastructure granular to faintly platey.

Brood-chamber lateral to macula centre, descending to inner edge of marginal lamina where probable oeciostome opens. Surface with sparse, shallow excavations and pores and kenozooidal openings at periphery; excavations usually with one or a few pores, these minute and closed by radial spokes. Oeciostome not obviously distinguishable from autozooidal peristomes; interpreted to be represented by transversely oval opening just above marginal lamina, 0.103 mm wide.

Ancestrula not seen.

Remarks. The species is based on the unique holotype colony from Puysegur Bank off the southwest coast of South Island, at 107 m depth. It is distinguished from all other species by its small size, the somewhat flat, elevated macula, and the lateral brood-chamber with an oeciostome that opens at the inner edge of the marginal lamina. *Disporella minima* Moyano, 1991 is comparable in its small size (not exceeding 2 mm in diameter, however) but has an inflated, sac-like gonozooid (Moyano 1991). *Lichenopora violacea* Canu and Bassler, 1927 has a similar-shaped colony with a high, flat-topped macula with a steep zone of autozooids around the edge, but the autozooidal apertures are arranged in connate, uniserial radii.

***Disporella novae-hollandiae* (d'Orbigny, 1853)**

(Figs 40–47)

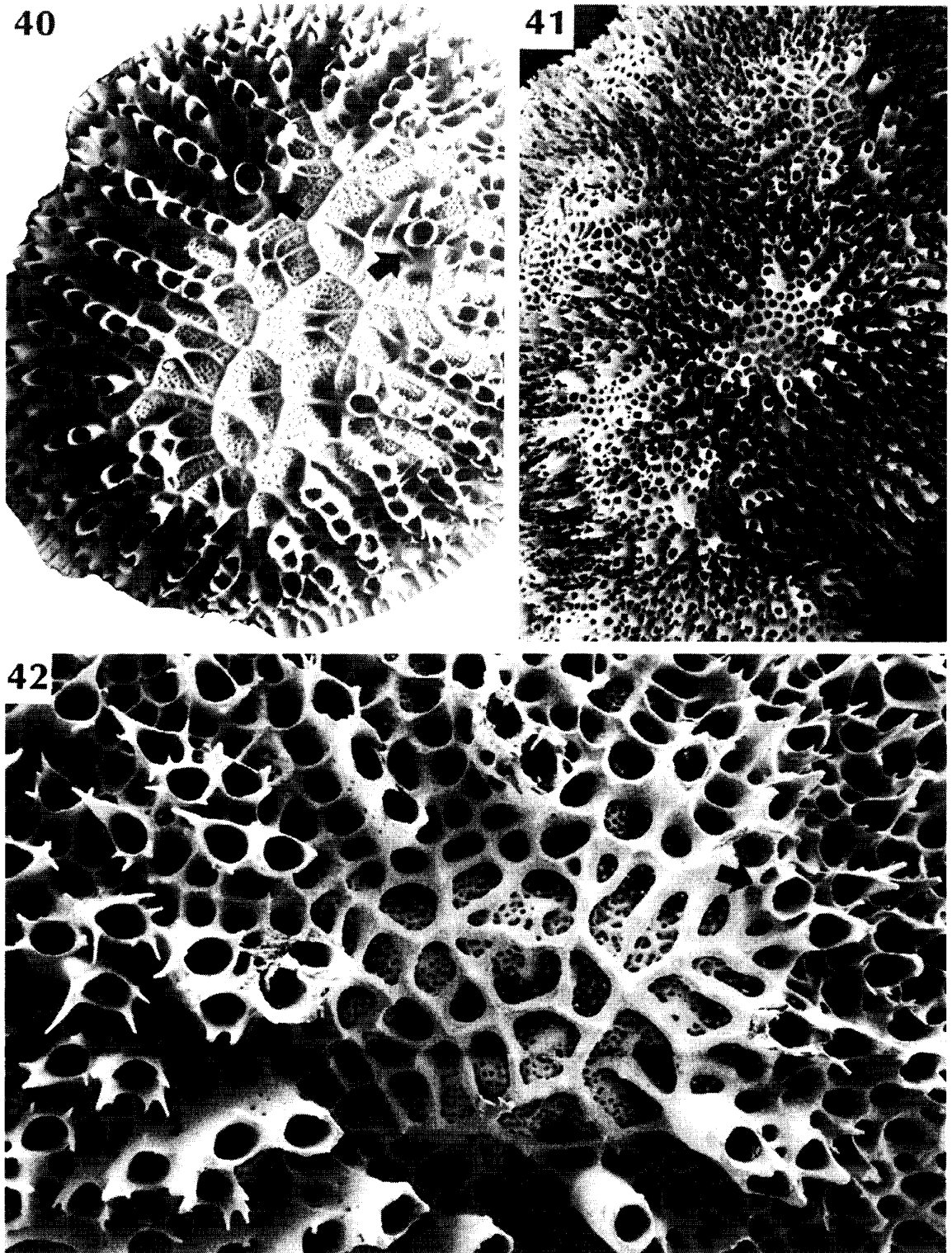
Unicavea novae-hollandiae d'Orbigny, 1853: 971.

Patinella verrucaria: Hutton 1873: 103. [Not Fabricius, erroneously attributed to Edwards]

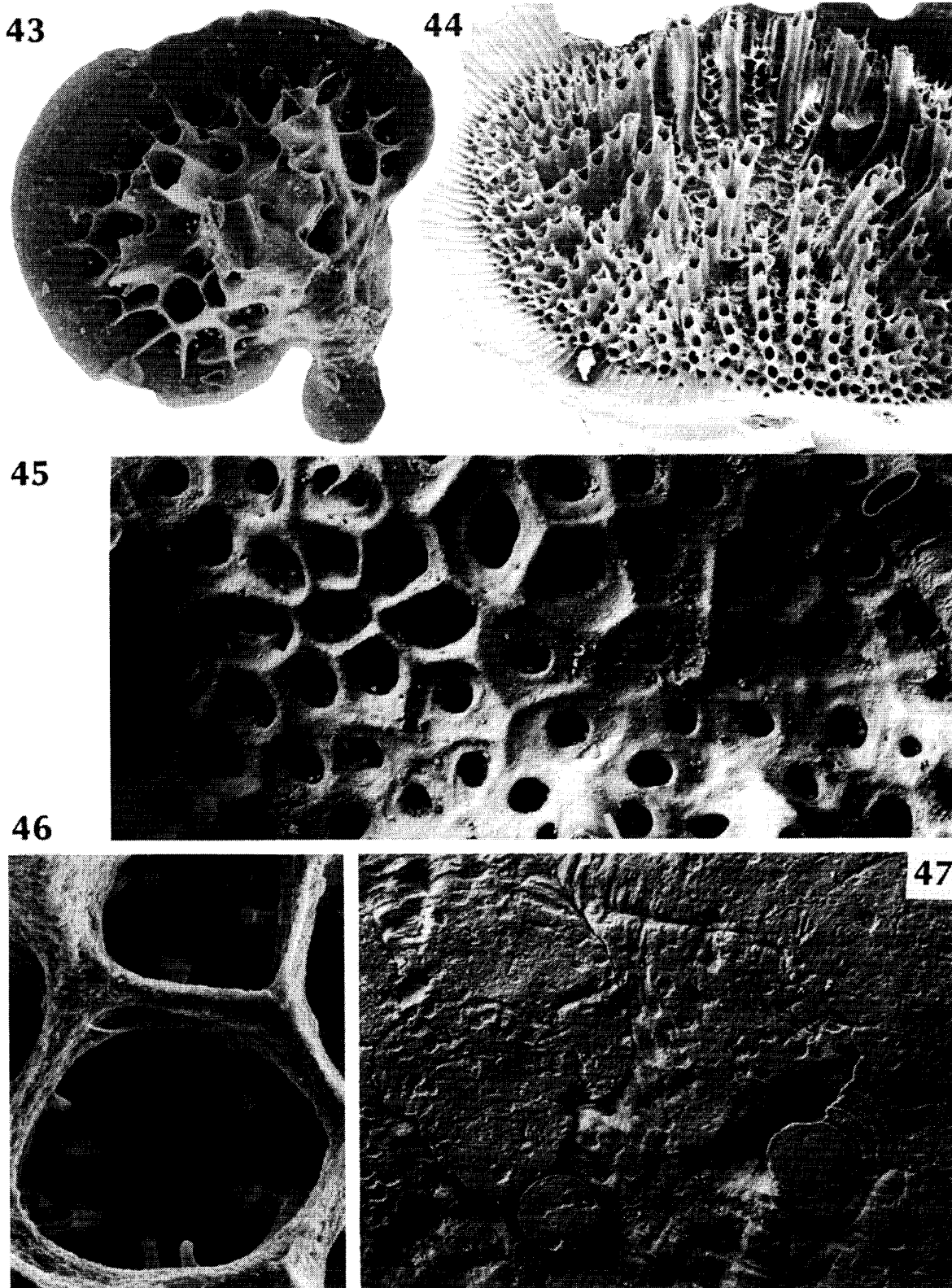
Discoporella novae-hollandiae: Busk 1875: 33.

Discoporella novae-zelandiae Busk, 1875: 32, pl. 30, fig. 2; Hutton 1877: 361; not 1878: 25 (*fide* Gordon and Parker 1991); 1880: 199; ?Haswell 1880: 353.

Lichenopora novae-zelandiae: ?Hincks 1884: 362; ?1887: 132; not Waters 1887a: 261, pl. 7, fig. 8; Jelly 1889: 137; ?Ortmann 1890: 65, pl. 2, fig. 10; Hamilton 1898: 197; not Jullien and Calvet 1903: 164; ?Thornely 1905: 127; Harmer 1915: 155 (part), pl. 12, figs 6–11; Okada 1917: 255; 1923: 220; ?Livingstone 1927: 69; ?Sakakura 1935: 117; not Marcus 1938: 198, fig. 6; Borg 1944: 222; ?Osburn 1953: 705, pl. 74, fig. 4; Brood 1976: 299, fig. 17A–C (not fig. 17G–I, = *Disporella sibogae* Borg); Hayward and



Figs 40–42. *Disporella novaehollandiae* (d'Orbigny, 1853). 40, D. P. Gordon Collection, Mission Bay, Auckland, from *Sargassum sinclairii*, simple colony with extensive brood-chamber, two oeciostomes visible (arrows), $\times 34$. 41–42, NIWA Stn Z8834, Tom Bowling Bay: 41, compound colony with several maculae, brood-chamber visible near upper right, $\times 13$; 42, brood-chamber of same colony enlarged, oeciostome at right (arrow), $\times 60$.



Figs 43–47. *Disporella novaehollandiae* (d'Orbigny, 1853). 43, D. P. Gordon Collection, Mission Bay, from *Sargassum sinclairii*, ancestrulate colony, $\times 49$. 44, NIWA Stn B498, Cook Strait, simple colony with tall peristomes, $\times 19$. 45–47, D. P. Gordon Collection, Mission Bay, Auckland: 45, kenozooids from centre of infertile colony, $\times 94$; 46, kenozooids with pinhead spinules (mural spines), $\times 360$; 47, underside of small, frontally compound colony derived from two ancestrulae, $\times 79$.

Cook 1983: 137; ?Mawatari 1986: 82, fig. 16; Winston 1986: 31; Alvarez 1993: 278, fig. 11A–D.

Lichenopora victoriensis Waters, 1889: 284, pl. 15, fig. 4.

Lichenopora neozelanica (sic): Hutton 1891: 107; 1904: 299.

Lichenopora holdsworthii: Hamilton 1898: 197. [Not Busk]

Lichenopora novae-hollandiae: Borg 1944: 222; Sabri 1988: 71, pl. 6, fig. 1.

Lichenopora novaezelandiae: Morton and Miller 1968: 226, figs 76, 214; Gordon and Ballantine 1977: 124.

Material examined. Holotype of *Discoporella novaezelandiae*, NHM 1875.5.29.48, Recent, New Zealand, collected by Dr Lyall. NIWA, unregistered colonies from New Zealand: Mission Bay, Auckland, on drift *Sargassum sinclairii*; Goat Island Bay, Leigh, North Island, on sandstone; NIWA Stns B235, B498, D273, K801, K871, M780, Q686, Z9684, Z9696, Z9701, Z9705.

Description. Colony simple, circular, and radially symmetrical, or subcircular to suboval, with single macula centre; or compound, irregular, with up to 20 or more maculae. Maculae very variable in size and relative spacing—central area of macula between opposing radii 0.56–1.13 mm in diameter in simple colonies (attaining 1.89 mm in one simple specimen); in compound colonies, entire maculae (central area plus radii) ranging from 0.75 to 1.13 mm, with adjacent centres 1.22–2.26 mm apart. Completely adnate, with entire basal surface affixed to substratum or with basal wall curving upwards at edges where substratum irregular or limited. In profile, small infertile colonies with centrally depressed region surrounded by zone of relatively steeply sloping, erect, radiating autozooidal tubes; tubes adjacent to colony centre slanted away from centre or occasionally vertical. Entire colony surrounded by thin marginal lamina. Simple colonies up to 5 mm in diameter including lamina; compound colonies up to 15 mm including lamina.

Surface of depressed colony centre comprising layer of relatively short kenozooids with polygonal outlines. Kenozooids initially thin-walled, with central cavity occupying almost entire opening, and diameter reduced to small, circular/subcircular hole by shelf-like thickening developing inside rim. Identical kenozooids also developed in interradii between autozooidal rows. Inner skeletal surface of kenozooids studded by pinhead spinules (mural spines); these mostly spiny-headed, but some lacking expanded head and appearing as thin tubercles.

Autozooids typically connate, in radiating, uniserial rows; occasionally ends of rows widening to two zooids. In simple colonies, some 20–21 major radii arranged with taller proximal ends surrounding colony centre, with roughly similar interradii distance between them; with increasing colony diameter, new radii interpolated between major ones, thus maintaining roughly similar interradii spacing. Mature simple colonies generally with 11–12 autozooids in each major radius, sometimes up to 14, and with 4–6 in shorter radii. All radii sloping quite steeply in height from colony centre to growing margin. In large compound colonies, maculae variable in shape and radial arrangement of autozooidal tubes less in evidence; radii shorter and many peristomes arranged quincuncially. Autozooidal apertures circular to radially oval, ranging from 0.078 mm in diameter in small colonies to 0.077×0.115 mm in diameter in large colonies; shape of apertural rim varying from relatively simple and mitriform to slightly fimbriated with 2–4 spines or cusps. Pinhead spinules visible deep in autozooidal interiors, especially

in relatively short, developing autozooids; mature autozooids generally with smooth inner walls or short, sparse tubercles. Outer faces of autozooids with pores. Polypides with 9–10 tentacles.

Marginal lamina with relatively long septa indicating vertical walls of incipient zooids; surface between lines smooth, with ultrastructure of imbricating platy crystallites.

Brood-chambers occurring in macular centres, with lobes between autozooidal radii. Brood-chamber floor covering central kenozooids and parts of lateral walls of adjacent autozooids. Single brood-chamber apparently in small colonies, with at least two in large colonies, judging from number of oeciostomes. Oeciostome typically situated adjacent to centralmost autozooidal peristome of excentric radius; its opening usually suboval, sometimes circular, occasionally flared, with short inner shelf on side adjacent to colony centre; external diameter 0.057×0.077 mm in small colonies, increasing in size proportionately in larger colonies to maximum external diameter of 0.135 mm.

Ancestrula with discrete, smooth-walled protoecium of 0.154 mm in diameter, its peristome partly adnate, with thin parallel lines of calcification. In small flabellate colony of 6–8 autozooids, at least one autozoid directed proximally and fold of calcification beginning to proceed backwards towards protoecium. Young colonies appearing to be radially symmetrical in frontal aspect, but basal surface showing excentricity of ancestrula; therefore, growth proceeding, at least initially, more distal to ancestrula than proximal to it.

Brood-chamber formation. Skeletally, brood-chambers form when a layer of calcification establishes the floor of the chamber, initially forming lobes between autozooidal radii and proceeding towards the colony centre. Floor calcification then curves upwards (frontalwards) on both sides to form the walls and then the densely pseudoporous roof. A thin ridge of calcification starts to form in the roof along the line of fusion of the lateral walls. Simultaneously, kenozooids are partitioned off in the spaces between lobes of the brood-chamber or between adjacent brood-chambers, in turn connecting with the ridges that mark the fusion lines. As kenozooidal walls increase in thickness and height, the mature brood-chamber surface acquires its characteristic reticulated appearance and the pores become occluded. At this stage, pinhead spinules develop on the brood-chamber roof to line the floor and walls of the kenozooids that develop over its surface. Inner walls of brood-chambers are densely studded with short, thin headless tubercles. The smallest colony with a completed brood chamber (only one oeciostome) was only 0.47 mm in diameter (including the marginal lamina).

Remarks. *Disporella novaehollandiae* is widespread in the New Zealand region, from Raoul Island (Kermadec Ridge) through northern North Island to Cook Strait and South Island to Foveaux Strait, from the low intertidal to 205 m depth on a range of substrata including stones, mollusc shells, and algae. Its wider distribution appears to include the Indo-Pacific from Japan through Indonesia, the Great Barrier Reef, southern Australia, East Africa, and South Africa.

D'Orbigny's species name *novaehollandiae* has occasionally been referred to in the literature (e.g., Busk 1875; Borg 1944) but its identity has not been known. Recently, Sabri (1988) illustrated a specimen in the d'Orbigny collection at the Muséum national d'Histoire naturelle, Paris, collected from Tasmania. This specimen (MNHN no. 13777), taken as holotype, was illustrated by SEM and redescribed.

We have also recently examined it. It has all the features typical of *D. novaezealandiae*, and is accepted here as a senior synonym.

Disporella novaehollandiae (under a variety of names) has for more than a century been included among the adnate species of "*Lichenopora*" auctt., i.e., *Patinella*, even by Borg (1944), who reintroduced *Disporella*. The development of the brood-chamber is typical of *Disporella*, however. The species has been accorded a wide distribution throughout the Indo-Pacific. Distinctive features include uniserial radii of connate autozooids and the presence of pinhead spinules. Judging from the within-colony and between-colony variability found in New Zealand specimens, most non-New Zealand records are probably correctly attributed to this species. One character that appears consistent, and which should help in discrimination of this species in future samples, is the internal ledge inside the oeciostome opening. Osburn's (1953) illustration of a specimen from the Pacific coast of North America (as *Lichenopora novaezealandiae*) appears not to be of this species; although very similar, the position of the oeciostome is not typical. Ryland and Hayward (1992) reported that non-compound colonies from Heron Island, Great Barrier Reef, "are typically oval and domed, and may reach 10 mm in length."

Dimensions of autozooidal peristomes in the New Zealand material (0.077–0.115 mm in diameter) agree with those measured in the holotype specimen of *Disporella novaezealandiae* (0.083–0.120 mm in external diameter) by Alvarez (1993). Harmer (1915) measured an oeciopore as 0.075 mm in diameter in a colony from Timor, which falls within the range (0.057–0.135 mm) for New Zealand specimens. He did not mention the internal ledge.

Busk (1875) described *D. novaezealandiae* as a "small species, rarely exceeding 1/8 inch [3.5 mm] in diameter" and "(? always on a *Catenicella*)". He cited the species as "abundant", but did not describe or illustrate the brood-chamber, which indicates he may have seen only simple infertile colonies. The species may indeed be found on catenicellids, as well as on the other substrata listed above. In Auckland Harbour, simple colonies of *D. novaehollandiae* are common to abundant on the fucoid alga *Sargassum sinclairii* (Morton and Miller 1968, figs 76, 214, as *Lichenopora*).

Compound colonies have not previously been reported but are common (along with simple colonies) on molluscan shell gravel in Spirits and Tom Bowling Bays at the northernmost tip of North Island. Apart from size, and the presence of multiple maculae, they agree in all respects with simple colonies. It is assumed that, as colonies develop, they may bud subcolonies where space is not constraining, but another possible reason for large size is fusion of genetically identical individuals derived from a pulse of larvae from a single parental colony. One case was discovered which, in frontal view, appeared to be a simple colony with an adjacent bud. The underside showed quite clearly that there were two ancestrulae but that the two colonies had fused seamlessly (Fig. 47).

A colony from NIWA Stn Z9696 (Spirits Bay, North Island) is in the form of a helicospiral tube, 17 mm long and mostly about 3.7 mm diameter, formed by the bryozoan in a symbiotic relationship with an occupant hermit crab. This is the first record of *D. novaehollandiae* in this kind of association, which is common around New Zealand, involving several species of bryozoans and hermit crabs, seldom obligately (Taylor *et al.* 1989; Taylor 1994). Maculae in this specimen are fre-

quently transversely elongate and relatively vertical, with the innermost autozooidal peristomes greatly thickened, as in symbiotic colonies of *D. pristis*.

Discoporella holdsworthii Busk, 1875 (type locality Sri Lanka), which also has uniserial autozooidal radii and denticulate pinhead spinules, has sometimes been confused with *D. novaehollandiae* (e.g., Hamilton 1898). Alvarez (1992) illustrated by SEM a fertile specimen from the type series; apart from having a more convex, domed colony profile, the outer brood-chamber surface is exterior-walled, i.e., gymnocystal. Accordingly, this species cannot be included in *Discoporella* or even the family Lichenoporidae as currently understood. We refer to this species as *Favosipora holdsworthii*, comb. nov. (Densiporidae) (see earlier).

According to Harmer (1915), Borg (1944), and Brood (1976), *Lichenopora victoriensis* Waters, 1889 is a junior synonym of *D. novaehollandiae* (as *L. novaezealandiae*). Gordon and Parker (1991) illustrated by SEM a fertile South Australian specimen, attributed by Hutton (1878) to *D. novaezealandiae*, in which simple oeciosomes are located at the distal ends of brood-chamber lobes, adjacent to the colony margin. On this character, the specimen appears not to be conspecific with *D. novaehollandiae*. Neither does it appear to be *D. victoriensis* (cf. Gordon and Parker 1991). Its identity is uncertain. In passing, it should be noted that Waters's (1889) reason for establishing *D. victoriensis* is questionable. In the first instance, it was introduced as a replacement name for *Discoporella reticulata* MacGillivray, 1884 on the grounds of homonymy with *Defrancia reticulata* von Hagenow, 1851. The last-named form is a Cretaceous species for which there is no evidence of the combination *Lichenopora reticulata* (von Hagenow) being used. Second, it is not certain that *D. victoriensis* Waters and *D. reticulata* MacGillivray are conspecific—MacGillivray (1884) stated that “there are no spines to be seen in the interior of any of the cells [autozooids] or cancelli [kenozooids]” of *D. reticulata*.

***Discoporella sacculus* sp. nov.**

(Figs 48–51)

Material examined. NIWA holotype H-744 from NIWA Stn Z9181 and paratypes P-1209, P-1210 from NIWA Stns S565 and Z9181; also a specimen from the Kermadec Ridge.

Etymology. Latin *sacculus*, bag, diminutive, used as a noun in apposition; alluding to the sac-like brood-chamber.

Description. Colony simple, circular, and mostly radially symmetrical, with single macula centre. Maximum diameter 5.0 mm including marginal lamina, 3.5 mm excluding lamina. Macula centre between opposing radii somewhat irregular in shape, measuring 1.89×1.23 mm in diameter in largest colony. Completely adnate, with basal surface affixed to substratum or with some upward curling of edge of marginal lamina. In profile, largest colony coronet-like within marginal lamina, i.e., with admaculate peristomes highest and colony centre sunken.

Macula centre occupied by kenozooids in infertile colonies, by kenozooids and proximal halves of brood-chambers in fertile colonies. Kenozooids relatively thick-walled, their openings of widest diameter (up to 0.15 mm but usually smaller) at colony periphery, becoming much reduced by wall thickening and/or closed by thin diaphragms. Interior of walls with sparse, needle-like spinules.

Autozooids quincuncial, peristomes projecting upwards around periphery of macula, increasingly facing laterally towards the marginal lamina; longest peristomes 0.79 mm including fimbriae. Apertures circular, 0.11 mm in diameter. Peristome opening elongated as projection on macular side, either unadorned or, where protected at growing edge, distally and laterally fimbriated; inner surface granular.

Marginal lamina generally with tiny, tubercle-like granulations, often in concentric rows marking former growth lines; ultrastructure of lamina surface platey.

Brood-chamber simple, formed like an elongate sac, aligned radially with its proximal end in macula centre and oeciostome opening near colony margin. Exterior surface of functioning brood-chambers with sparsely distributed pores with simple openings of variable diameter; oeciostome roundly D-shaped, 0.13–0.16 mm × 0.094–0.11 mm. Older non-functioning brood-chambers lacking open pores, surface often with radial line of small tubercles; oeciostome sealed by calcification.

Ancestrula not seen.

Remarks. *Disporella sacculus* is known only from deep water, from the slopes of the Norfolk and Kermadec Ridges and from the Bay of Plenty between 972 and 1350 m depth on hexactinellid sponge spicules. The most distinctive attribute of the species is the saccate brood-chambers. Presumably these develop sequentially; two small colonies have none, one larger colony has two, and another has three. In the latter colony these are arranged at roughly equal angles to each other, giving the macular centre a triradiate appearance; the oeciostome of the oldest brood-chamber in this colony is completely concealed by calcification, that of the next-oldest is visible but sealed, and that of the functioning brood-chamber is open.

The species is most reminiscent of another deep-sea lichenoporida, *Disporella minima* Moyano, 1991 from Chile, from 1200–1800 m depth. It, however, does not exceed 2 mm in diameter, even when fertile, and the saccate brood-chamber is single and more bulbous (Moyano 1991).

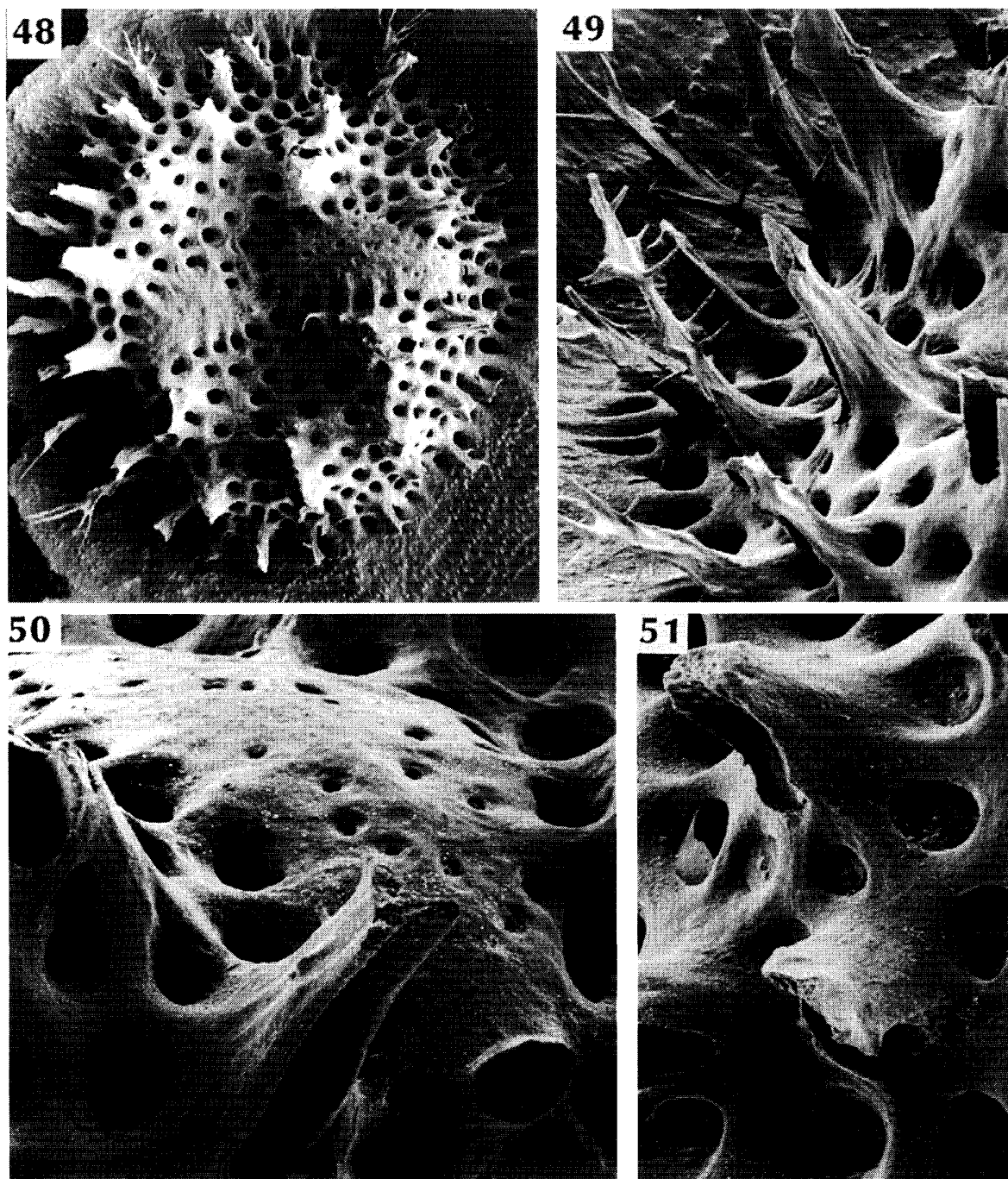
Genus *Doliocoitis* Buge and Tillier, 1977

Doliocoitis Buge and Tillier, 1977: 4.

Type species. *Doliocoitis atlantica* Buge and Tillier, 1977: 4, by monotypy.

Revised diagnosis. Colony thickly encrusting to mounded or suberect and claviform, maculae generally present. Autozooids and kenozooids opening at more or less same level, often of same diameter and wall thickness except for kenozooids having larger size range and attaining smaller diameters; autozooids sometimes distinguished by short peristomes with short apertural processes. Terminal diaphragms absent. Lateral walls tending to moniliform, with mural spinules or small pustules generally present. Brood-chamber interior-walled with definite floor, highly lobate and ramifying, visible at colony surface during development but rapidly becoming concealed by zooidal chambers developing across its surface.

Remarks. The genus *Doliocoitis* was established for a single claviform to barrel-shaped species from West Africa, attributed by Buge and Tillier (1977) to the cerioporine family Cerioporidae. Cerioporids in the strict sense, however, have exterior-walled brood-chambers that appear at the colony surface and do not develop



Figs 48–51. *Disporella sacculus* sp. nov., NIWA holotype H-744, Stn Z9181, Bay of Plenty, fertile holotype colony: 48, frontal view of colony with two sac-like brood-chambers opposite one another, middle left and right, respectively, $\times 17$; 49, elongate peristomial processes at colony margin, $\times 58$; 50, brood-chamber and oeciostome, $\times 96$; 51, kenozooidal diaphragms adjacent to autozooidal peristomes, $\times 216$.

kenozooids on the roof. For this reason, and because neither kenozooids nor autozooids develop terminal diaphragms, we provisionally include *Doliocoitis* in the Lichenoporidae. The genus appears to be close to *Disporella* but the type species is distinguishable by the sum of its characters, notably the absence or paucity of long autozooidal peristomes with fimbriae, the ephemeral appearance of the brood-chamber at the colony surface, and the thickness of the colony. The brood-chamber roof in *D. atlantica* also appears to have a solid rather than porous/alveolar construction, the significance of which needs to be investigated.

***Doliocoitis cyanea* sp. nov.**
(Figs 52–58)

“blue *Disporella*”: Taylor, Weedon and Jones 1995: 206, figs 1a, b, 2d, e, 3d, f, 5c, f.

Material examined. NIWA holotype H-746 and paratype P-1211 from Portobello Marine Laboratory Stn Mu88-32 and NIWA paratype P-1213 from NIWA Stn B236; also a colony from NIWA Stn B222.

Etymology. Latinised from the Greek, *kyaneos*, blue, referring to the colour of the colony.

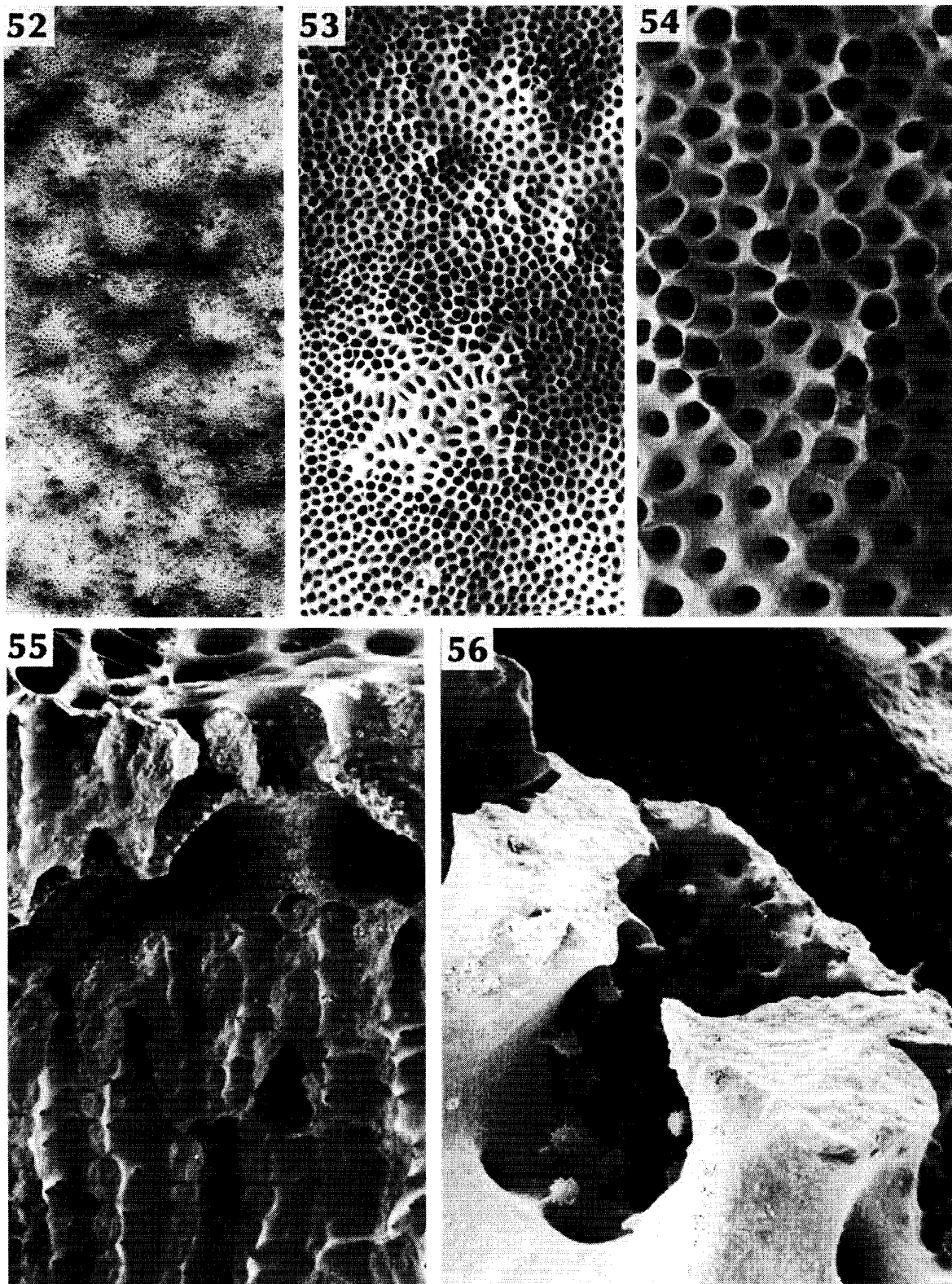
Description. Colony blue to purplish-blue, large, up to 30 mm in longest dimension and up to 4 mm thick, with up to ca. 65 maculae. Small colonies not seen. Maculae mostly around 1.0–1.5 mm in diameter but some smaller or larger, attaining up to 4.3×1.9 mm; centre-to-centre spacing ca. 1.5–2.0 mm. Colony adnate, with marginal lamina.

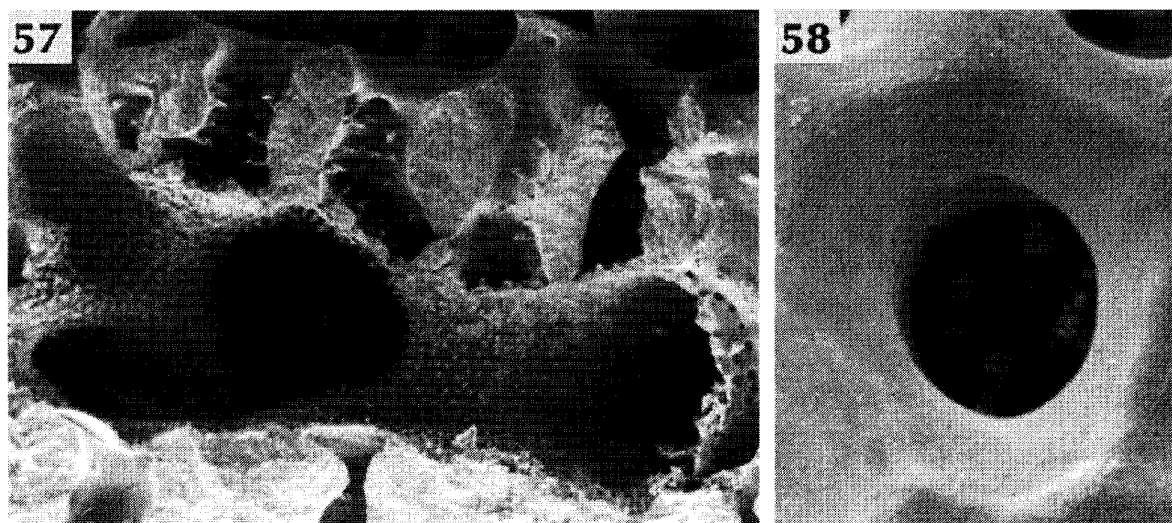
Kenozooids mostly 0.075–0.17 mm in external diameter, larger in macular centres and interradian areas than in intermacular areas, but increased wall thickness in macular centres reducing internal diameters to ca. 0.07 mm; elsewhere, as in intermacular areas, internal diameters ca. 0.058–0.10 mm.

Autozooids circular or polygonal, ca. 0.092–0.12 mm in internal diameter, or oval (as when in radii) and ca. 0.094–0.13×0.075–0.081 mm in internal length and width; arranged around macular centres in short, connate, uniserial radii of 2–6 peristomes or in small fascicles of 3–9 peristomes, apertural rims of those in radii tending to be produced into short process on abmacular side. Lateral walls of autozooids and kenozooids generally moniliform, indented at sites of interzooidal pores, these often with tiny septum in wall centre. Kenozooids externally easily differentiated from autozooids by smaller diameters and numerous denticulate pinhead spinules on inner wall; spinules sparser towards the interior of the zooid.

Marginal lamina smooth, skeletal ultrastructure of imbricating platey crystal-

Figs 52–56. *Doliocoitis cyanea* sp. nov., Portobello Marine Laboratory Stn Mu88-32, Otago Shelf. 52, part of large, 28 mm long, 3 mm thick, fertile NIWA holotype H-745, ×4.2. 53–56, NIWA paratype P-1211: 53, colony surface showing macular and intermacular areas, ×12; 54, macular and intermacular kenozooids with pinhead spinules and short series of autozooidal apertures lacking spinules (mural spines), ×38; 55, fractured colony showing zooids in longitudinal section and part of a brood-chamber just beneath the colony surface, ×67; 56, frontal view of short kenozooid above brood-chamber roof, chamber floor below with pustulose surface, ×310.





Figs 57–58. *Doliocoitis cyanea* sp. nov., NIWA paratype P-1211 from Portobello Marine Laboratory Stn Mu88-32, Otago Shelf: 57, lateral view of fractured subsurface brood-chamber, $\times 92$; 58, frontal view of a macular kenozooid, $\times 279$.

lites.

Brood-chambers concealed, not externally visible; internally irregular and highly ramifying, varying in chamber height and width from 0.094 to 0.38 mm in diameter. Brood-chamber wall distinct, evenly developed all round, sealing off zooidal chambers below and to sides, carpeted with dense granulations, some minutely spinulose. Chamber roof perforated by tiny pores, outer surface with pin-head spinules and pustules associated with overlying kenozooid layer. Oeciosomes not externally obvious—apparently represented by simple circular openings, slightly smaller than autozooidal apertures (ca. 0.087 mm in diameter), situated on sides of maculae between thickened kenozooidal walls.

Ancestrula not seen.

Remarks. This distinctively coloured species is known only from the Otago Shelf and eastern Foveaux Strait from 27 to 84 m depth on molluscan shell gravel. Its generic placement is not altogether certain. As mentioned above in the remarks on *Favosipora otagoensis*, the form of the brood-chamber in the type species of *Borgiella* is not known with certainty, which leaves only three other genera of thickly encrusting, free-walled cyclostomes as candidates for the present species. These are *Borgella* Kluge, 1952 [see also Kluge (1955)] (type species *B. tumulosa* Kluge, 1952), *Klugenotus* Androsova, 1982 (type species *Klugea capitonia* Androsova, 1965), and *Doliocoitis*. *Borgella tumulosa* and *B. pustulosa* (Osburn, 1953) have externally concealed, interior-walled brood-chambers that are pierced by autozooidal tubes, and the floor includes porous terminal diaphragms of underlying zooids. Neither of these characters is found in the present species. The brood-chamber of *Klugenotus capitonia* is unknown [Androsova (1965, 1982), and personal observation of type specimen]. *Klugea tuberculata* Androsova, 1965 has an exterior-walled brood-chamber like that of *Favosipora*. The well-developed, imperforate, subterminal diaphragms that occur in *K. capitonia* (personal observation of the type specimen) are a cerioporine character, and it is likely that *K. capitonia* and *K. tuberculata* are

not congeneric. [In passing, it should be noted that the interior-walled brood-chamber of *Borgella* is not characteristic of the Cerioporidae in the strict sense, and the encrusting colony form is not typical of the Corymboporidae (which has a similar brood-chamber), so there seems to be no current family available for this genus—unless the type species of *Borgiella* is confirmed to have an interior-walled brood-chamber, in which case the family Canuellidae Borg, 1944 may be available.]

On balance, then, *Doliocoitis* appears to be the nearest available genus for the present species, even though the genus is otherwise known only from the Western Atlantic north of the equator. If *Doliocoitis* is a lichenoporid, the family Cerioporidae remains unknown in the Atlantic Ocean north of latitude 34°S (see Androsova 1971).

Discussion

The genus *Favosipora* is now recognised to contain at least nine species, with only one definitely known from the Northern Hemisphere (Sri Lanka), the others ranging from southern Australia (two species), New Zealand (five species), and Chile (one species). In New Zealand, the genus ranges from the low intertidal zone to 104 m depth. Two species, New Zealand *F. candida* sp. nov. and Chilean *F. nanaoifera* (Moyano, 1982) have secondary nanozooids, a character more usually associated with tubuliporines. On the other hand, the combination of free-walled zooids and exterior-walled brood-chamber indicates a cerioporine organisational grade, while, as Weedon and Taylor (1996) have shown, the skeletal ultrastructure is more typical of rectangulates, and one of the two subgroups of cerioporines has the same ultrastructure (see also Taylor and Weedon 2000).

The New Zealand rectangulate fauna is increased by the addition of two new species of *Disporella* and one new species of *Doliocoitis*. While it has not been possible to follow brood-chamber development and view the brood-chamber floor in all of the New Zealand species, those characters that are obvious give evidence that *Patinella* is not present in the New Zealand fauna.

Key to the New Zealand Species of Densiporidae and Lichenoporidae (based on fertile colonies)

1. Brood-chamber exterior-walled (Densiporidae)..... 2
- Brood-chamber interior-walled (Lichenoporidae)..... 5
2. Pinhead spinules present in zooidal interiors *Favosipora rosea*
- Pinhead spinules absent 3
3. Nanozooids present in some parts of colony..... *Favosipora candida*
- Nanozooids absent..... 4
4. Colony mounded, with white monticular kenozooids separated by pigmented autozooids in furrows *Favosipora marmorosa*
- Colony comprising single macula, autozooids in 1–2-serial radii *Favosipora tinctoria*
5. Pinhead spinules present in zooidal interiors..... 6
- Pinhead spinules absent 7

6. Autozooidal peristomes elevated, in uniserial radii *Disporella novaehollandiae*
- Autozooidal peristomes scarcely or not at all elevated *Doliocoitis cyanea*
7. Colony compound, autozooidal peristomes fimbriate, entire surface minutely granular *Disporella pristis*
- Colony otherwise 8
8. Colony skeleton pink, autozooids in distinct, elevated radii *Disporella wanganuiensis*
- Colony skeleton white, autozooids arranged in quincunx 9
9. Autozooidal peristomes fimbriate, brood-chamber(s) central *Disporella sacculus*
- Autozooidal peristomes entire, brood-chamber marginal *Disporella humilis*

Acknowledgments

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Appendix

NIWA Station data (NI=North Island, SI=South Island)

B221: 21 May 1960, 46°40.00'S, 168°16.79'E, 31 m, Foveaux Strait
 B222: 21 May 1960, 46°30.00'S, 168°24.19'E, 27 m, Foveaux Strait
 B226: 21 May 1960, 46°55.00'S, 168°16.79'E, 49 m, Foveaux Strait
 B235: 23 May 1960, 46°34.99'S, 167°55.00'E, 49 m, Foveaux Strait
 B236: 23 May 1960, 46°34.99'S, 168°02.50'E, 36 m, Foveaux Strait
 B473: 3–4 June 1961, 43°20.0'S, 169°47.0'E, 215 m, Westland, SI
 B498: 11 June 1961, 40°46.30'S, 174°02.80'E, 44 m, Cook Strait
 D269: 6 October 1964, 40°44.5'S, 173°36.0'E, 57 m, Cook Strait
 D270: 6 October 1964, 40°40.0'S, 173°36.6'E, 62 m, Cook Strait
 D273: 6 October 1964, 40°45.0'S, 173°49.5'E, 75 m, Cook Strait
 E820: 23 October 1967, 46°35.0'S, 165°58.0'E, 220 m, Puysegur Bank, SI
 E821: 23 October 1967, 46°43.5'S, 165°46.5'E, 285–305 m, Puysegur Bank, SI
 G259: 23 January 1968, 43°32.99'S, 179°22.00'E, 419 m, Chatham Rise
 H57: 21 February 1970, 50°00.00'S, 167°01.99'E, 154 m, Auckland Islands Shelf
 K801: 22 July 1974, 29°14.7'S, 177°51.7'W, 18–22 m, Raoul Island, Kermadec Ridge
 K871: 2 August 1974, 31°21.25'S, 178°49.25'W, 10–47 m, Havre Rock, Kermadec Ridge
 M779: 31 March 1981, 44°36.0'S, 167°49.4'E, 30 m, Milford Sound, Fiordland, SI
 M780: 1 April 1981, 44°36.6'S, 167°52.1'E, 40 m, Milford Sound, Fiordland, SI
 Q686: 2 December 1981, 40°41.3'S, 174°03.8'E, 205 m, Cook Strait
 S565: 12 August 1983, 29°18.49'S, 169°46.69'E, 1350 m, west of Norfolk Island
 Y38: 16 March 1997, 46°08.22'S, 166°11.38'E, 107 m, Puysegur Bank, SI
 Z8468: 1 June 1996, ~34°24'S, 172°47'E, 40–50 m, Spirits Bay, northern NI

- Z8567: 18 October 1996, 36°59.05–52.90'S, 176°16.51–17.11'E, 395 m, Bay of Plenty, NI
 Z8639: 3 March 1996, 34°59.46'S, 173°58.20'E, 41 m, Cavalli Islands, northeast NI
 Z8645: 27 February 1997, 34°22.20'S, 172°48.00'E, 51 m, Spirits Bay, northern NI
 Z8664: 26 February 1997, 34°58.1'S, 173°45.5'E, 28 m, off Whangaroa Harbour, NI
 Z8834: 27 February 1997, 34°23.2'S, 172°52.0'E, 48 m, Tom Bowling Bay, northern NI
 Z8850: 2 March 1997, 34°47.1'S, 173°13.1'E, 36 m, Rangaunu Bay, northeast NI
 Z9181: 20 July 1998, 37°01.4'S, 176°43.1'E, 972–1207 m, Bay of Plenty, NI
 Z9221: 7 August 1998, 37°06.5'S, 176°36.8'E, 920–846 m, Bay of Plenty, NI
 Z9667: 24 January 1999, 34°24.31'S, 172°49.95'E, 29 m, Spirits Bay, northern NI
 Z9673: 25 January 1999, 34°17.38'S, 172°44.00'E, 85 m, Spirits Bay, northern NI
 Z9684: 26 January 1999, 34°23.55'S, 172°51.72'E, 40 m, Spirits Bay, northern NI
 Z9695: 27 January 1999, 34°22.00'S, 173°00.01'E, 89 m, Tom Bowling Bay, northern NI
 Z9696: 28 January 1999, 34°19.44'S, 172°44.94'E, 69 m, Spirits Bay, northern NI
 Z9701: 28 January 1999, 34°17.90'S, 172°47.55'E, 76 m, Spirits Bay, northern NI
 Z9705: 28 January 1999, 34°23.85'S, 172°47.55'E, 32 m, Spirits Bay, northern NI
 Z9707: 29 January 1999, 34°18.71'S, 172°42.01'E, 83 m, Spirits Bay, northern NI
 Z9715: 29 January 1999, 34°23.41'S, 172°59.17'E, 30 m, Tom Bowling Bay, northern NI
 Z9976: 30 December 1999, 43°22.32–24.08'S, 173°45.82–47.12'E, 118–124 m, Mernoo Saddle, SI

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